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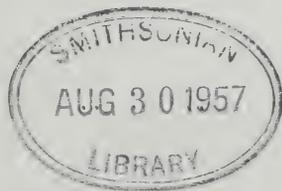
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A CONTRIBUTION TO THE EXPERIMENTAL TAXONOMY
OF *POA ANNUA* L.

By T. G. TUTIN
University of Leicester

INTRODUCTION

Poa annua is a grass which is all too familiar to most people. It is more abundant in the neighbourhood of habitations than anywhere else, being one of the commonest of garden weeds and forming the bulk of vegetation of suburban pavements. It also occurs in places less modified by man, though, as it is essentially a plant of open habitats, it is rather restricted and is practically absent from closed communities. Within these limitations it occupies a great variety of habitats, with the notable exception of salt-marshes. It can be found on stabilised dunes, in open turf on cliffs or near rock outcrops, at the margins of ponds and streams on bare mud or even in shallow water, and on the summits of mountains.

As is to be expected in a species capable of growing in such a diversity of habitats, a very considerable degree of variability is to be found and a number of varieties have been described (see, for example, Hegi, 1935, and Jansen, 1951). The nature of this variation has been investigated in four instances, and the first part of the present paper is concerned with this; in the second part the relationship between *P. annua* and two other species of *Poa* is considered.

INTRASPECIFIC VARIATION

The material used consisted of four stocks, three obtained from a garden in Leicester and the fourth from a somewhat moist depression in a sand-dune near Horsey in E. Norfolk. In the cultivation and hybridisation experiments all the plants of each stock used were grown from seed from a single parent plant.

The four stocks will be referred to as A, B, C and D and their chief distinguishing features are as follows :

A. Tufted, clear green. Leaves rather stiff, erect, 2-3 mm. wide. Stems erect or ascending, averaging about 15 cm. long. Longer panicle branches 2-3 cm. long; spikelets appressed to the rhachis, mostly with 4 florets, rarely with 3. Lowest lemma 2.7-3 mm. long with the mode at 3 mm. The most abundant form as a garden weed and in streets. This plant seems to correspond to var. *annua* (var. *typica* Beck). Plate 1 and Fig. 1, C.

B. Clear green. Stems creeping and rooting at the nodes then ascending, 20-30 cm. long. Leaves rather soft and drooping, 3-4 mm. wide. Panicle branches divaricate, longer ones 1.5-2.5 cm. long; spikelets spreading at a wide angle to the rhachis, with 4-5 florets. Lowest lemma 2.5-2.8 mm. long with the mode at 2.6 mm. Less common than A and found particularly on damp clayey soils and in wet places on mountains. ? var. *reptans* Hausskn. Plate 1.

C. Small tufts. Leaves dark green with purplish sheaths, rather stiff, 1.5-2 mm. wide. Stems spreading to ascending, about 5 cm., rarely up to 10 cm. long. Longer panicle branches 0.7-1 cm. long; spikelets purplish, slightly spreading, with 2-4 florets. Lowest lemma 2-2.4 mm. long with the mode at 2.3 mm. Rather uncommon, on firm dry soils. Plate 2.

D. Large very dwarf tufts. Leaves deep green, stiff, very short (1 cm. or less) and about 1 mm. wide. Stems geniculate, spreading to ascending, 3-7 cm. long, slender. Longer panicle branches 3-5 cm.; spikelets purplish, appressed to the rhachis, with 1-2, rarely 3 florets. Lowest lemma 1.8-2.2 mm. long with the mode at 2 mm. Moist places behind dunes. Plate 2 and Fig. 1, D.

The measurements given above are for average plants growing in good illumination on reasonably moist soils. There is, of course, considerable phenotypic variation which does not, however, obscure the differences between these 'races.' In shade the plants are taller with thinner leaves and long, often nodding panicles with few spikelets; the purplish colour of C is much reduced, sometimes the nodes alone showing it, but the leaves remain darker green than in A or B. In dry places or on poor soils A and C are both dwarfed, but the differences between them are, if anything, emphasised; B has not been found in such places.

A, B and C have been kept under observation for six years in the garden in which they grow as weeds. During this time they have remained distinct and no intermediates between them have been noticed. B and C are almost restricted to the same fairly small areas where they were first noticed six years ago, B in somewhat shady places with a very sticky always damp soil and C usually in full exposure on a heavy but well-drained soil. A is widespread and occurs, though not abundantly, in the habitats occupied by B and C; it can always be readily distinguished from them, and indeed the contrast between it and the dwarf purplish plants of C is very striking. These observations suggest that the differences between these 'races' are genotypic rather than phenotypic, and that cross-pollination rarely if ever occurs.

A study of anthesis in *P. annua* led Hackel (1904) to the conclusion that cross-pollination as well as self-pollination occurred. Since this conclusion is not supported by the evidence given above it seemed advisable to re-examine the process of pollination. Hackel's observations were confirmed and somewhat extended but, as will be seen, another interpretation of what happens is possible and appears to be more likely.

In *P. annua*, anthesis starts from the top of the panicle and proceeds downwards, and the same order is followed in the individual spikelets. The uppermost floret or, in the larger spikelets, the two upper florets, are always female, the remainder being hermaphrodite. The female florets open in the early morning and, apparently regularly, remain partially open with protruding stigmas during the following day. On the succeeding morning they again open widely and, according to Hackel, this may in exceptional circumstances be repeated for three or four days.

The behaviour of the hermaphrodite florets varies a certain amount in detail with variations in humidity and temperature but the following example makes the main points clear.

Two plants were observed in detail, one (E) in a pot, which was brought indoors at 5.45 A.M., G.M.T. and the other (F) in the open ground. The morning was a misty one in late August when there was a heavy dew.

At 5.45 all the florets, except a few female ones, were tightly closed, but by 6.10 the lemmas and paleas of F had started to separate and one panicle was cut and brought indoors (G). Five minutes later the stamens of G had elongated so that they were slightly shorter than the lemmas and stiffly erect. (The anthers remain erect on the rigid filaments until the latter begin to wither.) The stigmas emerged, spreading nearly horizontally. At 6.25 the anthers of G started to dehisce from the top downwards and were then slightly above the top of the lemma. The rather sparse pollen fell on to the stigmas and lemmas, though some grains remained in the anthers. The anthers of the upper hermaphrodite florets were about on a level with the stigmas of the female florets which were pollinated

by them. At 6.28 dehiscence was complete, and by 6.40 the filaments were withering. Meanwhile, by 6.20, E had begun to open and five minutes later the filaments were elongating, dehiscence following at 7.9.

Out of doors things moved more slowly, though between 6.30 and 6.35 a large number of plants, mostly of race A but including some examples of races B and C were seen to have fully elongated stamens. Dehiscence of the anthers in F and other plants in the open ground did not occur until about 7.30, when the sun broke through the mist. This delay of $1\frac{1}{4}$ hours between the extension of the filaments and the dehiscence of the anthers was unusually long, presumably because of the very high humidity. The hermaphrodite florets and the female ones, which had opened on the previous day, again closed gradually between 9.00 and 11.00. On wet days the anthers split but do not open wide; they, and the pollen, are beaten on to the top of the lemma, to which they stick, and pollen is washed in abundance on to the stigmas. In winter, cleistogamy is of frequent occurrence.

The features of anthesis in *P. annua* which would appear to favour self-pollination are:—

1. The flowers are homogamous (protandry appears to prevail in the majority of chasmogamous grasses).
2. The anthers are small (0.6–0.8 mm.) and are not versatile.
3. The filaments are rigid, until after most of the pollen is shed.
4. The amount of pollen is relatively small for a wind-pollinated plant (c. 800–1,000 grains per anther compared with something of the order of 10,000 per anther in *Brachypodium sylvaticum*) and the grains rather large (c. $32\ \mu$ in diameter).
5. The pollen is liberated not far from ground level and much of that which is not caught on the spikelets appears soon to reach the ground.
6. The pollen is shed very rapidly and almost simultaneously by all the plants in one area, so, even if some grains are carried about in the wind, the concentration of 'own' pollen must be very much greater than that of strange pollen.
7. In addition to the overlap between the anthers and stigmas of different florets in the same spikelet, neighbouring spikelets are often very close to each other at anthesis.

Even if self-pollination occasionally fails, the chance of true outbreeding, in the sense of crossing between different 'races', seems to be remote. This is because *P. annua* usually grows in patches, all the plants in which are most commonly the progeny of one parent plant which is likely to have been selfed.

As a further test for the view that selfing is the rule, the stigmas of 25 female florets from panicles in which no hermaphrodite florets had opened were examined. These florets were collected in the afternoon and were all ones which had already opened and from which the stigmas could be seen protruding. Not a single pollen grain was found on any of these stigmas, though a considerable amount of pollen must have been liberated the same morning from other panicles on the same plants and from other plants near at hand.

For comparison, stigmas from hermaphrodite florets, which had opened, were examined and on most of them 10–15 pollen grains were found, though, in one instance, there were as many as 38 grains. Thus, although the possibility of occasional crossing cannot be ruled out, it is evidently extremely rare.

One plant of each of races A, B and D was potted and put in a cold greenhouse. Panicles of each plant were covered before anthesis with bags of translucent paper which were folded round the culms and held securely in position by paper-clips until the seed was ripe.

A full set of good seed was obtained from all the covered panicles and samples were sown in sterilised soil on 12 June, 1952. A germinated in 10 days, B four days later and D seven days later. As soon as the seedlings were large enough to handle, 50 of each family, taken at random, were potted up in sterilised soil and the rest were discarded. The progeny of each plant was remarkably uniform and reproduced the characters of the parents, though there was a slight increase in size in 'race' D, presumably owing to the richness of the soil compared with that in the dune habitat of the parent.

This strongly supports the evidence from field observations that self-pollination is the rule and that the plants are therefore practically homozygous.

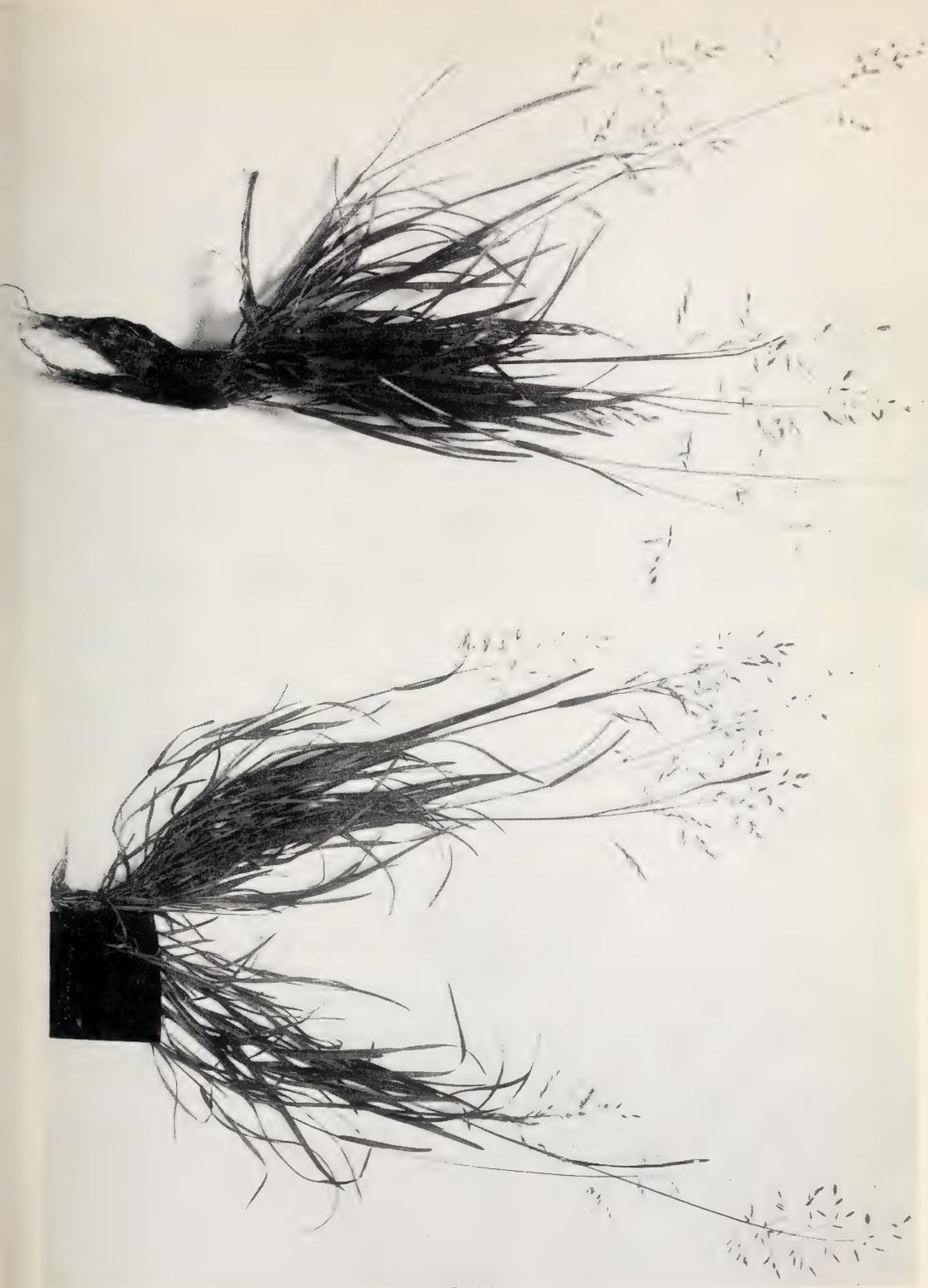
The differences between the rates of development of the 'races' were even greater than the differences between their speed of germination. By 30 August, i.e. 50 days after sowing, 92 per cent of the plants of race A were in full flower and were about 15 cm. high, while none of the plants of races B and D were showing any signs of flowering. The shoots of B were already spreading and rooting at the lower nodes and the plants were under 10 cm. high, while D was tufted and not more than 5 cm. high. Forty-five days later A had ripened one crop of seed but was still flowering sparsely. B was flowering, though the great majority of shoots was still in the vegetative state and most of the spikelets on the rather small, few-flowered panicles were viviparous. D was still entirely in the vegetative state and did not flower until early in the following summer, about eleven months after sowing. By this time the plants of A were dead. It is not possible to give an exact figure for the life-span of these different 'races,' since there is considerable variation between individuals in this respect, as well as variation with conditions. It is safe to say, however, that A and C only exceptionally live for as much as a year and normally have 2-3 generations in one year (Hackel, 1904), that B lives for at least 2 years and D for 3 years or more. There thus seems to be a correlation between the speed of germination, the time taken to arrive at reproductive maturity and the total length of life of the plant.

There are a number of other 'races' which almost certainly represent distinct genotypes, but which have not so far been investigated experimentally. Among these, two seem particularly well characterised by morphology and habitat; the shallow water form, var. *aquatica* Aschers., and the form found on the higher mountains.

The former grows up to 30 cm. or more high, with soft leaves, up to 4 mm. wide, which sometimes float on the water, when the whole plant rather resembles *Catabrosa aquatica*. The tufts are loose, with the stems spreading out at the base but not rooting at the nodes. The panicles are up to 7 cm. long and the longer branches up to 3 cm. The spikelets mostly have 4 florets and the lowest lemma is about 3 mm. long.

The mountain form occurs rather infrequently on stony slopes and damp rock ledges above 3,000 ft. in Scotland; along tracks and in the neighbourhood of cairns, dwarf specimens of var. *annua*, presumably introduced by man or sheep from lower levels, may also be found. The true mountain 'race' is tufted, with short broad leaves, rarely more than 1.5 cm. long but up to 3 mm. wide and often folded; the culms are stiffly erect and under 10 cm. high. One of the most characteristic features is the rather stout stem-bases with their covering of whitish, more or less coriaceous leaf-sheaths, somewhat reminiscent of *Poa alpina* on a small scale. The panicle is also characteristic, being short (usually 2 cm. long or less), dense, and having ascending or sometimes almost horizontal branches. The longest branches are 1 cm., or slightly more, with the rather broad brownish spikelets, each with 3-4 florets, densely clustered on them. The lemmas are broadly ovate with exceptionally prominent nerves, and the lowest is 2.6-2.9 mm. long. This race has the appearance of being perennial, but there is so far no certain information about this.

It has been suggested that perennation in *P. annua* is the result of a mycorrhizal



P. annua 'race' A. c. $\times \frac{1}{2}$ (top).
P. annua 'race' B. c. $\times \frac{1}{2}$ (bottom).

PLATE 4.



P. annua × *infirma*. × $\frac{1}{2}$ (bottom).
Possible artificial tetraploid from *P. infirma* × *supina*. × 1 (top).

infection. The breeding experiments with race B do not support this view, nor was Professor N. A. Burges able to find any fungus in the roots of this race.

It is thus evident that within *Poa annua* there are a number of infra-specific taxa differing both morphologically and in habitat and remaining distinct, probably owing to regular self-pollination. All the 'races' investigated are tetraploid with $2n = 28$, and are interfertile if artificially crossed. The situation is thus rather similar to that found in other, mainly autogamous, species such as *Senecio vulgaris*, *Capsella bursa-pastoris* and the *Bromus mollis* aggregate. These species are, however, all essentially weeds of cultivated ground and have a far smaller range of habitats, though *Senecio vulgaris*, for instance, does occur among natural vegetation on stabilised dunes. In their diversity of habitat and degree of morphological differentiation, the 'races' of *P. annua* perhaps resemble more closely the microspecies of an apomictic aggregate and if, as appears likely, we are dealing with a number of homozygous entities there is, in fact, little practical difference between autogamy and apomixis. The rank of such entities in the taxonomic hierarchy is perhaps best left for future consideration. If, however, subspecies are defined as taxa which differ from one another in minor morphological characters, and in ecology or in distribution, but which are potentially, though not normally, completely interfertile, then subspecies would seem to be the appropriate category in which to place these taxa which have for convenience been referred to as 'races.'

In the classification of the experimental taxonomist they would seem to fall into the category of ecotypes.

THE RELATIONSHIPS OF *POA ANNUA**

P. annua belongs to the rather small section *Ochlopoa* Aschers. & Graebn. (*Annuae* Fr., *Obsoletae* Rouy, *Vagantes* Döll) with six known species in Europe and N. Africa, all of which are rather similar morphologically. The chromosome number of *P. annua* has been determined by a number of workers (Stählin, Avdulov, and Kattermann, quoted in Nannfeldt, 1937; Litardière, 1938); the remaining species have been counted by Nannfeldt and counts have also been made on the material used in the present investigation; no deviations from the numbers given have been found. There are two diploid species with $2n = 14$, *P. infirma* Kunth (*P. exilis* (Tomm.) Murb.) and *P. supina* Schrader, the remaining four species, *P. annua* L., *P. dimorphantha* Murbeck, *P. maroccana* Nannfeldt and *P. rivulorum* Maire & Trabut, being tetraploids with $2n = 28$. An account of these species and a key for distinguishing them is given by Nannfeldt (1938). The last three tetraploids appear to be confined to N.W. Africa where they are rather local. Morphologically, and apparently genetically, *P. dimorphantha* is an isolated species, while *P. maroccana* resembles the diploid *P. infirma* and *P. rivulorum* is similar to *P. supina*; *P. maroccana* gives a sterile hybrid with *P. annua* (Nannfeldt, 1938).

P. annua itself is as nearly cosmopolitan as any phanerogam is, occurring throughout the north and south temperate regions even on small and isolated islands such as the Azores, and in the tropics on mountains and in the neighbourhood of towns. It is also to be found near dwellings within the Arctic Circle, and, at the other extreme, in Tierra del Fuego.

P. infirma (Plate 2 and fig. 1 A) occurs throughout much of the Mediterranean region and extends up the west coast of Europe to the Channel Islands, Scilly Islands and the Lizard peninsula in S.W. Cornwall. It is also found in S. America, where it has no doubt been introduced from Spain.

P. supina (Plate 3 and fig. 1 B), in contrast to the other diploid, occurs in Central and

* A brief summary of this section has already been published (Tutin, 1954).

Northern Europe and mainly in mountainous regions. It extends roughly from Spain to the Carpathians and north to Sweden, Poland and Siberia and is also reported from Abyssinia. Its exact distribution is somewhat uncertain as it has sometimes been confused with *P. annua* var. ? *reptans*.

As Nannfeldt (1937) has pointed out, *Poa annua*, though very variable, is in many respects intermediate between the two diploid species, though it has a far greater 'ecological amplitude' than either. The following table (modified from Nannfeldt) provides a comparison between the three species.

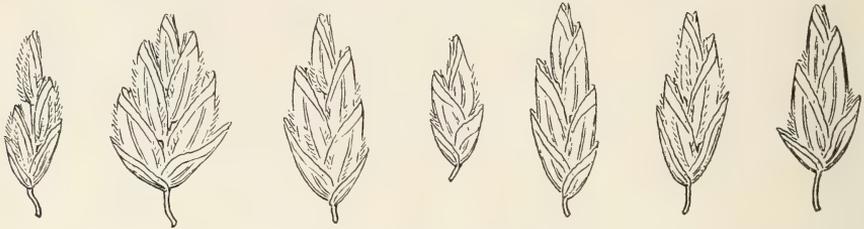


Fig. 1. Spikelets of *Poa* (from left to right): A - *P. infirma* (Channel Is.); B - *P. supina* (Switzerland); C - *P. annua* var. *annua* (Leicester); D - *P. annua* var. (Horsey); E ? *P. infirma* × *supina* (4n); F - *P. annua* × *infirma* (3n); G - *P. annua* × *supina* (3n). All × 5.

TABLE 1.

Character	<i>P. infirma</i>	<i>P. annua</i>	<i>P. supina</i>
Colour of plant	Pale yellow-green	Variable	Dark green and purplish
Panicle	Rather narrowly oblong, 1.5-3 times as long as broad; spikelets along whole length of branches	Oblong-triangular, 1.2-1.6 times as long as broad; spikelets ± uniformly spread along branches	Triangular, about as long as broad; spikelets clustered at end of branches
Panicle branches	Always ascending	Lower horizontal or deflexed after flowering	All but uppermost horizontal or deflexed
Spikelets	Nearly always devoid of anthocyanin	Variable but usually with some anthocyanin	Nearly always dark purple
Florets	Widely separated; uppermost slightly longer than pedicel, hermaphrodite	Less distant; uppermost twice as long as pedicel, female	Close together; uppermost 5-6 times as long as pedicel, female
Nerves of lemma	All with dense appressed hairs	Hairiness variable, sometimes glabrous	Glabrous, except for keel and margins
Anthers	0.22-0.4 mm. long	0.6-0.8 (-1.0) mm. long	1.6-2.0 (-2.5) mm. long
Dia. of pollen grains	c. 28.5 μ	c. 31.5 μ	c. 28.8 μ
Duration	Ephemeral	Ephemeral, annual or short-lived perennial	Perennial
Flowering times	March-April (in Britain)	January-December	Early summer

It therefore seems likely on morphological grounds that *P. annua* is an allotetraploid derived from the hybrid *P. infirma* × *supina*.

That a relationship exists between *P. annua* and *P. supina* is shown by the occurrence of a hybrid between them, first recognised by Nannfeldt (1935), who showed it to be, as expected, a sterile triploid. In an attempt to obtain further evidence about the possible hybrid origin of *P. annua*, he investigated the idiograms of the hybrid and its parents, and of *P. infirma*, but found that analysis of somatic metaphase in the triploid and tetraploid was almost impossible. Attempts to obtain the hybrid *P. infirma* × *supina* by open pollination of the former in early anthesis by the latter were also unsuccessful.

In April 1949, a supply of seed of *P. infirma* was collected from St. Brelade's Bay, Jersey, where the plant is abundant in short turf near the sea. Some of this seed was sown in the early summer of 1949, but did not germinate till autumn. A further sample was sown early in the spring of 1950 and germinated rapidly in a slightly warmed greenhouse. These two lots of *P. infirma* flowered in March-April and May-June respectively. The second lot was used for hybridising with *P. annua*. Two plants of this, taken from race A (see Plate 3) were used. On these approximately 60 florets were emasculated, using a binocular dissecting microscope and a magnification of $\times 8.75$; the remaining spikelets were cut off, the plants repotted and the emasculated panicles covered. The plants were kept in a cold greenhouse, carefully weeded for other *P. annua* plants, and were pollinated daily for a fortnight with *P. infirma* pollen. Four seeds were obtained and these were sown in June, as soon as ripe, in sterilised soil; two germinated rapidly and reached maturity. One of these proved to be *P. annua*, presumably resulting from a failure to remove all the anthers completely, but the other was sterile with $2n = 21$ and was evidently the hybrid.

The following description of the hybrid was made on 1 August, when it had been flowering for about a fortnight.

P. annua \times *infirma* (Plate 4). Plant c. 15 cm. high. Leaves c. 2 mm. wide, tapering gradually to an acuminate apex, rather bluish green and firmer in texture than *P. infirma*, mostly smooth but a few with transverse wrinkles as in *P. annua*. Panicles up to 5 cm. long, lower branches spreading at about 70° in flower, later ascending at $20-30^\circ$. Uppermost floret about twice as long as its pedicel. Lemmas purplish at tip, silky on the nerves. Anthers 0.7 mm long, not dehiscent but remaining for some time projecting prominently from the florets, Pollen abortive. Spikelets (fig. 1 F) almost completely sterile, one inviable fruit being found, and therefore withering, but not breaking up, when old.

As previously reported briefly (Tutin, 1952), meiosis in the pollen mother cells of this hybrid showed seven bivalents and seven univalents. This indicated a high degree of homology between the chromosomes of *P. infirma* and one genome of the tetraploid *P. annua*.

In August 1951 a plant of *P. supina* was obtained, through the kindness of the late Dr. Walo Koch, from Alp Trida near Samaun, Graubünden, Switzerland. This, *P. annua* and *P. infirma* were all in flower in a greenhouse by 12 April 1952. On that date 100 florets of *P. supina* were emasculated, the large anthers making this a relatively easy operation. The panicles were covered and later pollinated from plants of *P. infirma* grown from seed sent by Mr. J. E. Raven from Porthloo, St. Mary's, Scilly Islands, in March 1950. The following day 78 florets of 'race' A, *P. annua* were emasculated, covered and subsequently pollinated from the plant of *P. supina*. The seed from these 78 florets was sown in sterilised soil and 31 plants were obtained, one of which soon died. Of the remainder, 28 plants proved to be the hybrid described by Nannfeldt (Plate 3, and fig. 1 G), and two were *P. annua*, the result presumably of accidental selfing. Meiosis in the hybrids was examined and again seven bivalents and seven univalents were found.

From the cross, *P. infirma* \times *supina*, seven seeds were obtained. These were sown in sterilised soil in June and three germinated in a fortnight. The seedlings grew very slowly for a time, but after about six weeks the growth of two of them became more rapid and one of these flowered at the end of August and the other early in October. Both these plants were found to be tetraploid and were morphologically rather similar to *P. annua*, though they did not match exactly with any local 'race' of that species (Plate 4 and fig. 1 E).

Mr. C. E. Hubbard, to whom a specimen was submitted without any information about its possible origin, comments as follows: "The lemmas differ from those of

typical *Poa annua* L. in being perfectly glabrous; there is no sign of hairs – not even of minute outgrowths on the keel ($\times 50$). The keels of the paleas are also only very slightly and obscurely ciliate about the middle third, the hairs being few and \pm appressed. The anthers are 0.8–1 mm. long. Your specimen is very similar indeed to material from England which I have included under *Poa annua* L. (*sensu lato*). It matches specimens from several places, including some from the allotments behind the Herbarium here.”

The meiosis of the majority of pollen mother cells examined was normal, but in a few cases a single quadrivalent was observed. About 12% of the seed produced by these plants was obviously shrunken and bad. A hundred apparently sound seeds from one and 250 from the other were sown in sterilised soil and of these 35% and 43.2% respectively germinated. After two further generations no shrunken seed was produced and germination had risen to between 95% and 100%, being mostly 98–99%. The third seedling continued to grow slowly and eventually proved to be *P. supina*, the result of accidental selfing.

It is unfortunately not possible to be absolutely certain of the mode of origin of the tetraploid plants, as no determination of the chromosome number was made in the early stages. This was not done because it seemed undesirable to disturb the very small seedlings, and also because it was anticipated that if they were of hybrid origin they would prove to be diploid. If this had been so, it had been intended to try the effect of colchicine on some of the growing points.

The possibility of their origin from stray seed must be considered. This seems highly unlikely for a number of reasons. Sterilised soil and clean pots were used throughout, and the greenhouse was kept free from wild *P. annua*. If seed had blown in, the chances of a single seed arriving in each of two pots at about the time the supposed hybrid seed was sown, and then of no more chance seeds arriving during the next four months, are very small. Further, the plants obtained did not match exactly with wild *P. annua* in the neighbourhood, showed occasional abnormalities at meiosis, and the seed from them had less than half the normal germination-rate of *P. annua*.

The most likely hypothesis that can be put forward is that the seedlings were at first diploid and grew very slowly until chromosome doubling occurred, when the tetraploid cells displayed the vigour which often characterises polyploids, and started to grow at a more normal rate.

There are thus a number of different pieces of evidence, none absolutely conclusive in itself, which taken together make it practically certain that *Poa annua* is an allotetraploid derived from the hybrid between *P. infirma* and *P. supina*.

Litardière (1939) favours the view that *P. annua* “dérive d’une mutation du subsp. *exilis* (i.e. *P. infirma*) occasionée par une duplication chromosomique.” This hypothesis seems unlikely, since an autotetraploid would probably show quadrivalents at meiosis. The chromosome pairing in the hybrid, *P. annua* \times *supina*, and the intermediate morphology and increased variability of *P. annua* all favour an allotetraploid origin.

In support of the autotetraploid hypothesis, Litardière (*l.c.*) points out that the two diploid species do not at present appear to overlap in their distributions and also differ fairly widely in their habitat preferences. It is not, however, difficult to imagine conditions under which they might have come in contact. During the Quaternary glaciations, *P. supina* would presumably have been driven down to low altitudes on the northern shores of the Mediterranean, particularly in places where mountains occur not far from the coast. During one of the warmer interglacials, or perhaps at the end of the last glaciation, when the ice was melting rapidly and quite high temperatures were probably attained in summer not far from the ice edge, *P. infirma* might well have spread rapidly into freshly available habitats. Thus it would be likely to come in contact with *P. supina* which, being a perennial, would persist for some time in its glacial refuges. That *P. supina* can persist

under fairly warm lowland conditions, is shown by the fact that the plant obtained from Switzerland is still alive after 5 years in a cool greenhouse.

It therefore seems possible that isolated colonies of *P. supina* surrounded by *P. infirma* occurred in one or more of the warmer periods in the Quaternary ice age. The more or less open plant communities, which appear to have been characteristic of the earlier parts of these periods, would provide a good opportunity for the survival of any hybrids which might have occurred between these two species. If spontaneous chromosome doubling then gave rise to *P. annua*, its vigour and versatility would ensure its establishment.

It therefore seems reasonable to suggest that *P. annua* is a species of recent origin and that it probably arose on the north side of the Mediterranean. Its recent origin is also suggested by the apparently perfect pairing of the seven bivalents in the two triploid hybrids. The chance of structural changes in the chromosomes or of mutations, which would prevent perfect pairing, is likely to increase with the age of the species.

If this hypothesis is correct, *P. annua* must have spread rapidly to have attained its present world-wide distribution. This rapid spread can be readily accounted for by its association with man; wherever it occurs in parts of the world far removed from its probable place of origin, *P. annua* appears to be always confined to tracks, gardens and the neighbourhood of habitations and to be an annual or ephemeral plant. It also seems to be always associated with man or with crop plants of European origin, and its occurrence in places uninfluenced by European man (if any still exist) has yet to be proved.

In Europe and Western Asia, the capacity of some of its 'races' for growing in a variety of natural habitats has given it a wider range; these 'races' not only lack the easy and rapid means of transport available to the weed varieties, but are also mostly perennial, and their occurrence in other countries has not been recorded.

Poa annua is, in fact, supreme among weeds for a number of reasons. It shows greater phenotypic and genotypic variability than most, if not all, others; it flowers and fruits throughout the year; it germinates rapidly, is small enough to escape notice and is not particularly easy to uproot; it also has great powers of survival when uprooted and thrown down. Its 'seeds' are readily dispersed in mud sticking to shoes, feet, implements or garden crops and its self-fertility and rapid life-cycle ensure that a single plant is enough to build up a large population in the course of a year or two.

The unusually great range of variation in duration and habit, as well as morphology, suggests that the present population of *P. annua* is not derived from one single hybrid, but from a number of different ones. The chances of hybridisation are obviously greatly increased when foreign pollen only is available, but the production of two plants, apparently of hybrid origin, from 100 emasculated florets of *P. supina* indicated that the fertility of this cross is high enough to make it possible for it to have occurred several times in nature. The fact, that the uppermost floret in each spikelet of *P. supina* is female and generally opens a day before the first hermaphrodite one, would also aid natural hybridisation.

Specimens of the material used in this investigation, and of the artificial hybrids, are in the Herbarium of the University of Leicester.

SUMMARY

1. A number of true-breeding 'races' of *Poa annua* are described.
2. These differ in minor morphological characters, in speed of germination, rate of development and life-span.
3. It is shown that while crossing between these 'races' is possible, it is at most extremely rare in nature.
4. A description of anthesis in *P. annua* is given.

5. *P. annua* is a tetraploid intermediate in many ways between the diploids, *P. infirma* and *P. supina*. The distributions and chief characteristics of these three species are given.
6. Hybrids between the tetraploid and each of the diploids were obtained and were found to be triploid. Meiosis in the pollen mother cells of these hybrids showed, in each case, seven univalents and seven bivalents, indicating a close genetical relationship between the diploid and the tetraploid.
7. A hundred florets of *P. supina* were emasculated and pollinated with pollen from *P. infirma*. Three viable seeds were obtained, one of which produced a plant of the female parent, while the other two produced tetraploids resembling *P. annua*.
8. The two tetraploids had generally normal meiosis, but occasionally a single quadrivalent occurred. Nevertheless, over half the seed produced was inviable.
9. In the course of three generations, the germination-rate had risen to between 95% and 100%, the normal for *P. annua*.
10. The origin of these tetraploids is discussed and it is concluded that they most probably arose through spontaneous chromosome doubling in diploid hybrids.
11. The morphological evidence, the evidence from meiosis in the triploid hybrids and the probable production of *P. annua*-like tetraploids from the hybrid between the diploids make it practically certain that *P. annua* is an allotetraploid derived from the two diploids.
12. It is suggested that *P. annua* arose on the northern side of the Mediterranean in the Late Glacial or during an Interglacial, and owes its present distribution largely to human migrations and its own exceptional suitability for growth in disturbed habitats. It is also suggested that it may have arisen on a number of different occasions.

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CYTOTAXONOMICAL STUDIES IN THE *CHRYSANTHEMUM LEUCANTHEMUM* COMPLEX

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The Ox-eye Daisy is very polymorphic and a large number of infraspecific taxa have been described by various authors (see, e.g. Briquet & Cavillier, 1916, 86-88, and Horvatić, 1935). The polymorphy undoubtedly is most striking when material from various parts of the whole range is considered. In a small area like Denmark the variation appears to be moderate. In the years 1949-56, we have collected material in various European countries for experimental cultivation and chromosome studies. In this material we were able to confirm the euploid series of chromosome numbers, $2n = 18, 36$ and 54 found by Dowrick (1952) in material from botanical gardens. The three cytotypes, however, apparently rarely occurred in the same area, suggesting three geographically distinct series of races. Dowrick (1952) states that there are no significant changes in form, apart from size and growth-rate, with increase in the degree of polyploidy and does not consider the cytotypes to be separate species. In our experiments, however, it is quite apparent that most diploids differ from the tetraploids in life-form (duration of life) and in some morphological characters. A taxonomic separation between the cytotypes, therefore, is not at all out of the question but an exhaustive systematic treatment must be postponed until more cultivation experiments and observations can be taken into consideration. The present paper only touches on some of the more important taxonomical questions. It is hoped that the differences which are reported below may prove stimulating and invite further studies. We should very much like to receive information which might complete our present knowledge of the distribution and should further be grateful to anyone who would supply us with seed collected in nature, accompanied by some notes about the habitat and the locality.

CHROMOSOME COUNTS PUBLISHED BY PREVIOUS WRITERS

The tetraploid number $2n = 36$ was first reported by Tahara (1915, 1921) who studied plants of unknown origin. It was further found by Orth, in 1926 (Tischler, 1950), by Shimotomai (1938) in material from Innsbruck and Kaiserstuhl, by Cooper and Mahony (1935) in var. *pinnatifidum* from N. America, and by Dowrick (1952) in garden material. The diploid number, $2n = 18$, also reported by Dowrick, was first found by Polya (1950) in Hungarian material from the province Hajdú-Bihar (along a railway bank). Quite recently Duckert and Favarger (1956) found $2n = 18$ in var. *alpicola* Gremli from the Jura. The hexaploid number was found by Dowrick (1952) in garden material.

CHROMOSOME COUNTS IN THE PLANTS USED FOR EXPERIMENTAL CULTIVATION

1. *Diploids*. Nine diploid strains were studied (see Table 1). In one of these, No. 3490 from Denmark, a small fragment chromosome occurred. During diakinesis it was frequently attached to the end of a rod-shaped bivalent. Duckert & Favarger (1956) found a rather high frequency of meiotic irregularities in the diploid var. *alpicola*. In

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Fig. 1. Distribution in Europe of the three cytotypes in the *Chrysanthemum leucanthemum* complex. Rings : Diploids (*C. leucanthemum* L.); Solid dots : Tetraploids (*C. ircutianum* Turcz.). Asterisk : Hexaploids (*C. pallens* Gay).

culture the diploid plants were frequently short-lived perennials and flowered in the first year of cultivation. After luxuriant flowering in the second summer, they died or were very much weakened and died after the third summer. None of the diploid strains was perennial, when cultivated in the experimental field. In nature the diploid population in Naesby Dale (No. 2733) was covering the hill slopes one year (Böcher, Christensen and Christiansen 1946, Fig. 3 and Plate 6, Fig. 1) while some few years later the plants in the same spot were scattered and of subordinate importance.

2. *Tetraploids*. Fifteen strains were counted in root tip mitoses and one (from Mösseberg) in meiotic divisions (Table 1). Meiosis appeared to be completely regular and no multivalent formation could be detected. Most strains were raised from seeds. Among these one from Småland (No. 3581) deviated by producing flowering heads on 5 out of 15 plants the first summer and by being inclined to die after flowering the second summer (10 out of 15). In the other 8 strains (1648-4180), the first-year plants remained vegetative, five of them being clearly perennials, whereas the rest, which flowered for the first time in the summer of 1956, are apparently perennials forming vigorous new basal shoots in the autumn.

3. *Hexaploids*. In one strain from Portugal (No. 3700) the number $2n = 54$ was counted. It belongs to subsp. *pallens* (Gay) Briq. & Cavill. The seedlings deviated by being much larger than those of the tetraploid strains. None of the plants showed any crowding of the basal leaves, as is usually the case with diploids and tetraploids, and they flowered abundantly in August the first year. After flowering most of the plants survived and flowered again in the next two summers.

POLLEN SIZE

In Table 1 all pollen measurements are put together. It appears that the diploid and tetraploid number to some extent corresponds to two different pollen sizes. However, a great overlapping exists, for which reason pollen size cannot be used in a simple way as a character by which herbarium material can be divided. In the two Danish tetraploids the pollen diameters are remarkably low. The hexaploid (No. 3700) has pollen of about the same size as the tetraploids, and this is also the case with some herbarium material of subsp. *pallens* from Southern Europe.

DISTRIBUTION OF DIPLOIDS AND TETRAPLOIDS

In Fig. 1 all stations for *Chrysanthemum leucanthemum* s.l. with known chromosome number are summarised. From the map and some additional pollen measurements from various stations (e.g., several from the British Isles) we are inclined to draw the conclusion that the diploids are prevailing in the north-west and the tetraploids in the north and east and in the mountains in the south, whereas both types occur intermixed in Central Europe. A distribution like this suggests two series of races, one diploid and with atlantic distribution and another tetraploid with continental-montane distribution. Much more material, however, is required in order to establish the distribution and frequency-limits of the two series. In Denmark, Eire, Jersey and, according to Duckart & Favarger, also in the Jura, the diploids frequently occur in natural plant communities whereas tetraploids, at least in Denmark, may have been introduced recently by man. In south-east Europe things may be quite different; tetraploids in Yugoslavia grew in natural meadows whereas the diploid found by Polya occurred along a railway.

TAXONOMY

The hexaploid subsp. *pallens* in our opinion deviates so much, that it seems natural with Gay in Perreymond (1833) to regard it as a separate species (*C. pallens* Gay). The diploid and tetraploid series of races might also be regarded as two species, but a clear-cut morphological distinction is made very difficult because some diploid varieties (e.g., var. *alpicola* Gremlé) approach the tetraploids morphologically. However, the majority of tetraploids can be clearly distinguished; they correspond to subsp. *montanum* (All.)

PLATE 5.



Fig. 1. Cultivated specimen of No. 3170 from Edenderry, Eire. Diploid series (= *C. leucanthemum* L. s. str.).



Fig. 2. Cultivated specimen of No. 7180 from Zagorsk, U.S.S.R. Tetraploid series (= *C. ircutianum* Turcz. s.l.)



Fig. 1.
Type specimen
of *Chrysanthemum*
leucanthemum L.
in British Museum.



Fig. 2.
The specimen of *Chrysanthemum*
leucanthemum in the Linnean Herbarium
(= *C. irtutianum* Turcz. s.l.).

Briq. & Cavill. although in some of the strains the small membranous calyx or crown may be rudimentary or even missing. This character, which has been used as a primary distinguishing feature by all previous taxonomists, does not correspond to the chromosomal differences and may therefore be regarded as a secondary one. It is possible on the basis of our experimental cultivations to describe two species, one covering most diploids and the other most of the tetraploids. The position of var. *alpicola* and a similar diploid race from Denmark as well as of the tetraploid var. *pinnatifidum* deserves a closer study, but it may prove correct to attach them to the diploid and tetraploid species respectively. The correct names for the two species seem to be *C. leucanthemum* L. and *C. ircutianum* Turcz.

Chrysanthemum leucanthemum L. (s. str.) 1753, *Species Plantarum*, 888 Syn.: *Leucanthemum vulgare* Lamk. subsp. *triviale* Briq. & Cavill. Diagnosis in Linnaeus, 1737, *Hortus Cliffortianus*. Type in British Museum (Natural History) (see Plate 6, Fig. 1). The type specimen is defective without any stem leaves. The pollen-size corresponds very well to that of the diploid strains (Table 1) and the basal leaves have to a great extent alternate, not opposite teeth or lobes. Thus it has two of the most important characters of our diploid series. The specimen in the Linnean Herbarium (No. 1012.7) which is shown on Plate 6, Fig. 2, belongs to a later collection. Its pollen-size (Table 1) and the regularly toothed stem leaves agree very well with corresponding features in our tetraploid plants.

The more important characters of *C. leucanthemum* L. are the following: Diploid, with small pollen, c. 27–33 μ in diameter (including spines on the surface). Lower leaves frequently subpinnatifid, more or less spatulate with irregular alternating lobes or teeth; upper leaves linear-lanceolate with pinnatifid bases not very regularly toothed. One or; few heads, 4–7 cm. in diameter (discs 1.5–2.7 cm. in diameter). Ray-florets with a limb 0.3–0.7 cm. broad and usually without crown or with this rudimentary or unilateral. Inclined to be a short-lived perennial at least in culture. Frequent in north-west Europe. Variable, including several subspecies and varieties.

Chrysanthemum ircutianum Turcz. (s.l.), 1846, *Bull. Soc. Nat. Mosc.*, **29**, II, 177 and *Cat. Pl. Baic. Dah.*, 605. Syn. *Leucanthemum ircutianum* (Turcz.) DC., *Prodromus*, **6**, 47, and Ledebour, *Flora Rossica* **2**, 543. Type: In pratis graminosis prope Irkutsk. In the descriptions this species is stated to be closely related to *Chrysanthemum montanum* sensu All., 1785, *Flora Pedemont.*, **1**, 190, tab. 37, fig. 2, from which it is distinguished by its upper leaves which are obtuse or subacute, not mucronate, and by the ray-florets which are longer. We have studied these characters in material of *C. ircutianum* in the Botanical Museum of Copenhagen and have been unable to separate this species from specimens of *C. leucanthemum* subsp. *montanum* or from our tetraploid specimens. (*C. montanum* L. is quite a different species.)

This species has the following important characters: Tetraploid, with larger pollen grains, c. 30–39 μ in diameter. Lower leaves spatulate to spatulate-lanceolate, regularly toothed and not lobed; upper leaves lanceolate (oblong-lanceolate to linear-lanceolate) regularly and mostly closely toothed, not or slightly pinnatifid at the base. Heads frequently more than one, 5–7.5 cm. (discs 1.5–3.0 cm.) in diameter. Ray-florets with a limb 0.4–0.8 cm. broad and frequently with a more or less distinct crown. Perennial, occurring in north-east Europe and Siberia as well as in European mountains. Variable, including several subspecies and varieties.

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CHROMOSOME NUMBERS OF
SAROTHAMNUS SCOPARIUS (L.) WIMMER

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Sarothamnus scoparius exists in erect and prostrate forms, the latter being referred to as subsp. *prostratus* (Bailey) Tutin by Tutin (1952), who states that it maintains its characters in cultivation and breeds true. He later (1953) points out that it should be called subsp. *maritimus* (Rouy) Ulbrich.

Morton (1955) figures and describes the chromosomes of both these subspecies, using, however, material from only one locality for each: from Longtown, Cumberland for subsp. *scoparius*, and from The Lizard, Cornwall, for subsp. *maritimus*. He claims that subsp. *scoparius* (the common subspecies) is tetraploid with $2n = 48$, and that subsp. *maritimus* is diploid with $2n = 24$. Camera lucida drawings of root-tip metaphase plates are included showing both chromosome number and morphology.

Böcher and Larsen (1955) confirm the statement of several other workers that subsp. *scoparius* is tetraploid with $2n = 48$, though they omit reference to a published British count of $2n = 46$ from Maude (1940), subsequently quoted by Tutin (1952). They continue: "but recently Morton (1955) has shown that material of subsp. *prostratus* from The Lizard, Cornwall, has only $2n = 24$. The senior author had an opportunity to study this interesting form at Three Castles Head in Eire, and at Grosnez Point in Jersey. From the latter station seeds were brought home, and some few plants were raised which had the prostrate growth habit. Strangely, however, they proved to be tetraploid ($2n = 48$) as was the case of all our cultures from many different stations in Europe."



Fig. 1

Sarothamnus scoparius subsp. *maritimus* metaphase—some supercontraction evident. Spindle inhibitor used.

Recently (1956) I germinated seeds of the prostrate form from the colony near the Lizard Head lighthouse, Cornwall, and unlike Morton, I found the tetraploid number, $2n = 48$.

The study was based upon root-tip squashes from the germinating seeds. α -bromonaphthalene was added to Knop's culture solution, and emulsified with a rapid stream

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of oxygen. The germinating seeds were added and incubated at 25–30°C. for one hour. The root-tips were fixed in Carnoy with chloroform and, after maceration, squashed in acetic-orcëin. All seedlings examined, grown from seeds from most of the plants in the sampled colony, appeared to be tetraploid, an actual count of $2n = 48$ being obtained. Similar squashes but without the use of the spindle-inhibitor also gave $2n = c. 48$.

These counts for subsp. *maritimus* from the Lizard, Cornwall, confirm those of Böcher and Larsen, and make it clear that the prostrate form is not invariably diploid.

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THE VARIETIES OF *RANUNCULUS FLAMMULA* L. AND THE STATUS OF *R. SCOTICUS* E. S. MARSHALL AND OF *R. REPTANS* L.

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The great number of varieties of *R. flammula* L. which have been described gives an indication of the morphological diversity found within this species. There are, in addition, two closely related taxa which have been given specific rank, *Ranunculus reptans* and *Ranunculus scoticus*. An attempt has been made to elucidate the status of these, and to evaluate the named varieties by experimental means and by study of the literature. This investigation has been carried out almost entirely upon British material, although Scandinavian and Icelandic specimens were used whilst studying *R. reptans*.

NOMENCLATURE.

The brief Linnean description of *R. flammula* covers a considerable range of variation, but the specimen in the Linnean Herbarium fortunately represents one of the commonest and most widespread forms of this species. In addition to this variety, *R. flammula* subsp. *flammula* var. *flammula*, a considerable number of other forms and varieties have been described within subsp. *flammula*. Many of these can be reduced to synonymy by an examination of the literature.

The following infra-specific names need further consideration :

1. var. *tenuifolius* Wallr. (1822) (var. *pseudo-reptans* Syme (1856), var. *gracilis* Meyer (1890), var. *radicans* Nolte (1830), var. *reptans* Neilr. (1859), *R. reptans* Maly (non L.)).
2. var. *angustifolius* Wallr. (1822).
3. var. *ovatus* Pers. (1807) (var. *latifolius* Wallr. (1822)).
4. var. *serratus* DC. (1818).
5. var. *natans* Pers. (1807) (forma *natans* Glück (1911)).
6. forma *submersus* Glück (1911).
7. var. *major* Schult. It has not been possible to determine the precise date of this description but it is certainly much earlier than var. *alismifolius* Glaab (1911) with which it appears to be synonymous.
8. var. *pilifer* G. Beck (1890).
9. forma *minimus* A. Benn. (1904).

Most of these taxa are defined by characters of habit, leaf shape and serration, and petiole length, alone.

Field observations and transplant experiments demonstrate clearly the plasticity of habit and of leaf shape and serration and petiole length. Except in var. *major* and forma *minimus* there do not appear to be any other morphological or anatomical characters that are correlated with the diverse leaf forms that occur in various habitats. It is therefore evident that taxa within subsp. *flammula* which are based solely on leaf form have little significance.

Within subsp. *flammula* it appears only to be possible to recognise, if desired, several forms which are in fact phenotypes. Of the forms of var. *flammula*, the plant characteristic of stony lake-shores is common and widespread in the north; it is small,

slender and prostrate, with stems that creep and root at most of the lower nodes. Plants of this type have a diploid chromosome number of 32 and fully fertile pollen. Specimens from a wide range of localities in the British Isles have been brought into cultivation; in all cases, the plants increased considerably in size and stoutness before dying down in the autumn, and the flowering axis produced in the following growing season was erect and showed no tendency towards nodal rooting. Field observations indicate that the small size and other characteristics are due to lack of nutrition, rather than to pH or drought. This phenotype will be referred to as forma *tenuifolius*.

Other distinct-looking phenotypes are forma *natans* (Pers.) Glück and forma *submersus* Glück.

Var. *major* Schult. is a strikingly large plant which has sometimes been confused with *R. lingua*. It was thought that this was essentially a southern plant, and that its large size was due to the milder climate of these areas; during the course of this investigation, however, specimens have been seen from most parts of the British Isles, the northernmost from Aberdeenshire. When cultivated, such plants retain the morphological characteristics which make them so conspicuous in the field.

Forma *minimus* A. Benn. has a number of inheritable characters which seem to justify its separation from subsp. *flammula* as a distinct subspecies. A description of it is given on p. 21

DESCRIPTIONS.

R. flammula L.

Perennial herb; stems (4 —) 8–55 (— 80) cm., erect or creeping and rooting at the nodes, uppermost part slightly branched. Laminae of basal leaves 0.5–4.0 (— 5.0) × 0.2–2.5 (— 3.0) cm., stalked, subulate or lanceolate to broadly ovate, base cordate to rounded. Laminae of cauline leaves 2.0–5.0 × 0.8–2.0 cm., stalked or sessile, ovate-

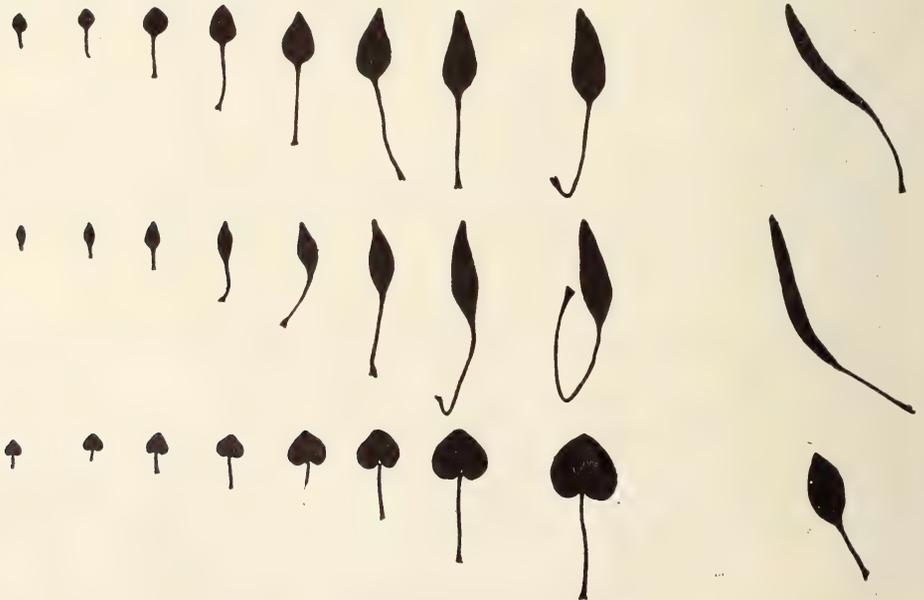


Fig. 1. Top and middle : Leaves 1-7, last basal leaf and leaf from second cauline internode of two plants of *R. flammula* subsp. *flammula*. Bottom : Corresponding leaves from a plant of *R. flammula* subsp. *minimus*.

lanceolate to linear-lanceolate. Leaf-margins subentire to strongly serrate. Flowers 1.8–2.0 (– 2.5) cm. diam. Sepals 5, greenish-yellow; petals 5, yellow, glossy, obovate. Achenes in a globose head of 20–50 (– 60), ovate, shortly beaked, 1.0–1.9 (– 2.2) mm. long (excluding beak). Ratio achene length : achene width = 1 : 1.4 (– 1.6); beak 0.05–0.39 (– 0.46) mm. long, slightly curved. Protandrous. Fl. 5–9. $2n = 32$.

Subsp. *flammula*.

Stem 8–55 (– 80) cm. long, erect or creeping and rooting at the lower nodes. Laminae of basal leaves 1.0–4.0 (– 5.0) × 0.8–2.5 (– 3.0) cm., stalked, lanceolate to broadly ovate. Ratio of achene length : achene width = 1 : 1.4.

Var. *flammula*.

Stem ascending or creeping and rooting. Plant fairly slender, flowers 0.8–2.0 cm. diam. 'Forma *tenuifolius*': stems creeping and rooting at the nodes; pollen fertile. 'Forma *natans*'; basal leaves long-petioled, laminae floating; plants growing in running water. 'Forma *submersus*' is a deep-water state which has submerged, narrowly elliptical leaves and is always barren.

Var. *major* Schult.

Erect robust plant rarely rooting at even the lowermost nodes, 35–60 cm. high. Laminae of basal leaves 3.5–5.0 × 2.5–3.0 cm. Cauline leaves correspondingly large. Flowers 1.8–2.5 cm. diam.

Var. *pilifer* G. Beck is said to be more or less densely clothed with hairs and would seem to be a distinct entity which is absent from this country.

R. flammula subsp. **minimus** (A. Benn.) P. A. Padmore subsp. nov., based on *R. flammula* forma *minimus* A. Bennett, 1904, Ann. Scot. Nat. Hist., 1904, 227.

The distinguishing characters of this taxon as described by A. Bennett are its small size, short internodes and the fact that the laminae shorter in proportion to the petioles.

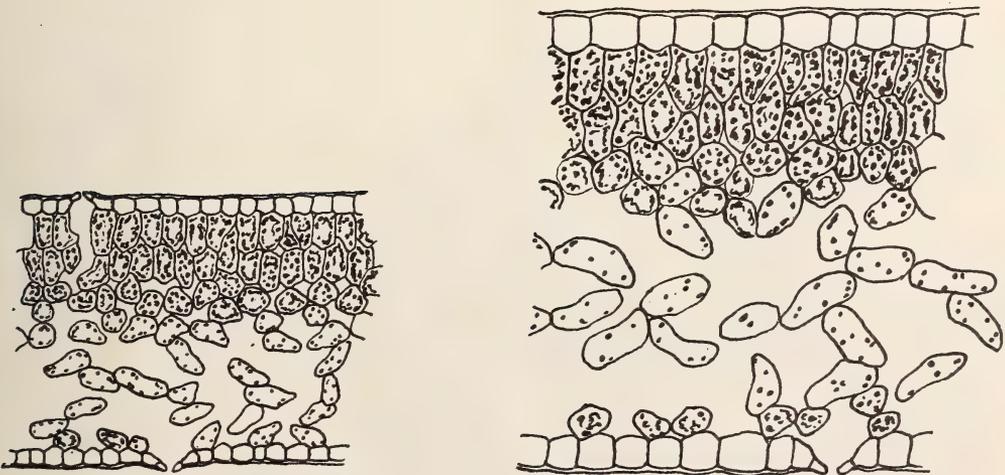


Fig. 2. T.S. leaf of *R. flammula* subsp. *minimus* (right) and subsp. *flammula* (left). × 38.

Stem semi-prostrate but not rooting at the nodes, 3-8 (-14) cm. long with very short internodes, 0.5-2.0 cm. long (those of subsp. *flammula* 4-7 cm.). Basal leaves shortly stalked, broader than long or at least orbicular, distinctly cordate at the base, thick and fleshy. Stem leaves broader in relation to length than in subsp. *flammula*. First flower at the second or third node (4th-7th in subsp. *flammula*). Flower diameter greater than 1.5 cm. Achenes 1.05 times as long as broad. The type specimen was collected from North Uist; other specimens labelled forma *minimus* by Bennett come from Holburn Head and the Cliffs of Kilkee.

Habitat: exposed situations by the sea, growing in short turf and often forming dense mats. Distribution: v.c. 109, Caithness, Holburn Head: v.c. 110, Outer Hebrides, North Uist: v.c. 111, Orkney, Yescanby and Skail Bay, v.c. 112, Zetland, Wick of Shuni: v.c. H9, Clare, Cliffs of Kilkee.

The most distinctive features of this plant are the short internodes, thick fleshy leaves and comparatively large flowers. The following table indicates the most important differences between these plants and normal *R. flammula*.

subsp. <i>minimus</i>	subsp. <i>flammula</i>
1. Basal leaves broader than long or at least orbicular.	Basal leaves longer than broad.
2. Basal leaves distinctly cordate at base.	Basal leaves cuneate, rounded or slightly cordate at base.
3. Leaves thick and fleshy.	Leaves thinner.
4. Internodes 0.5-2.0 cm. long.	Internodes 4-7 cm. long.
5. Height 3-8 (-14) cm.	Height usually considerably above 12 cm.
6. First flower from second or third node.	First flower from fourth to seventh node.
7. Flower diam. more than 1.5 cm. (large for the size of the plant).	Flower diam. 0.7-1.8 cm.
8. Achenes 1.05 times as long as broad.	Achenes 1.35 times as long as broad.

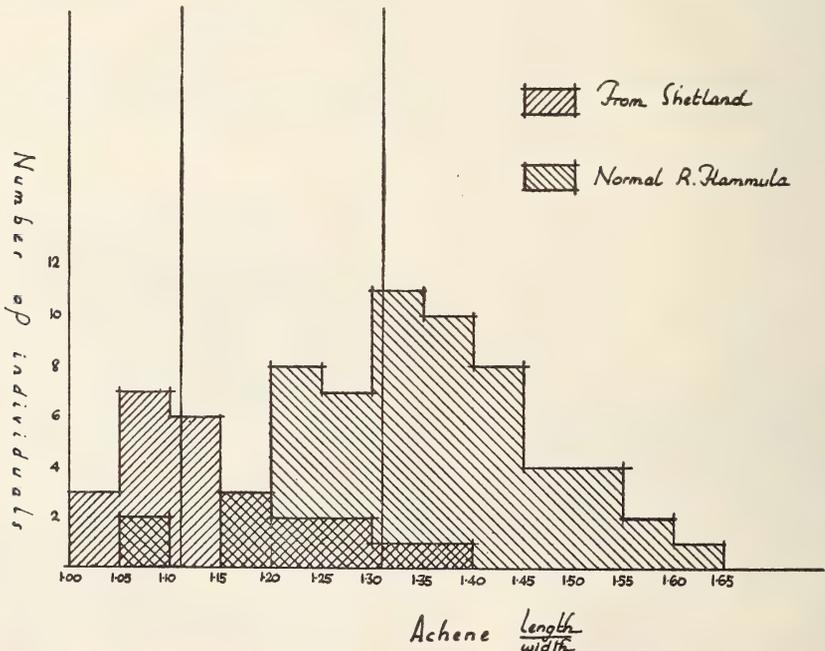


Fig. 3. Histogram of achene length : width ratio in normal *R. flammula* and the subsp. *minimus* from Shetland.

Plants from Orkney and Shetland were brought into cultivation in 1953; after 12 months they showed no morphological changes, apart from a slight increase in size which can be attributed to the richer soil conditions and reduced exposure. Seeds from these specimens were sown at the same time as seeds from two plants of normal *R. flammula*, and, as the leaves matured, they were removed in order and their silhouettes recorded. The results of this experiment are set out in Fig. 1 and indicate quite clearly that there is a marked difference between the two sets of seedlings. The plants were grown in artificial heat and light and their dimensions are therefore larger than they would be in the field.

Study of the leaf anatomy shows that the greater thickness of the leaves of subsp. *minimus* is due partly to larger cell size but mainly to an increase in the number of layers of cells (Fig. 2).

The accompanying histogram (Fig. 3) indicates that the mode of the ratio, achene length : achene width, is very much less in these plants (1.11) than in normal *R. flammula* (1.31). These results have been tested and found to be statistically significant.

While examining material in the British Museum, it was observed that some specimens collected by H. H. Johnston in Orkney had unusually large achenes. Even to the naked eye they appeared to fall outside the range of normal *R. flammula* achenes. This locality was visited in 1953 and live plants obtained which were brought into cultivation. The lengths of the achenes were measured under a dissecting microscope and the results plotted in the form of a histogram. This was compared with a similar histogram which had been prepared with the intention of obtaining a picture of the achene dimensions of the species as a whole, using achenes from a wide range of morphological types and from as many localities as possible. As can be seen from the accompanying diagram (Fig. 4) there is a marked difference between the two samples. These results have been tested and found to be statistically significant. There seem to be no other morphological characteristics to distinguish these plants from any other specimens of *R. flammula*. They are certainly above average size, but when the achene size of specimens of var. *major* was checked it was found to be in no way abnormal and indeed much smaller than in the Orkney plant. Cytological examination has shown a normal chromosome complement of $2n = 32$. No taxonomic status can be assigned to the plant until more is known about its morphology and distribution.

RANUNCULUS SCOTICUS

R. scoticus was first discovered by E. S. Marshall at Lochan Mathair Etive, Argyll (v.c. 98) in 1888. It was first described as *R. flammula* var. *petiolaris* Lange (Marshall, 1889), and then raised to specific rank as *R. petiolaris* (Marshall, 1892). This name was subsequently found to be pre-occupied and was therefore changed to *R. scoticus* (Marshall, 1898). The plant has subsequently been reported from numerous localities in N.W. Scotland and W. Ireland, but in many cases the identification has been incorrect.

The most striking character of this plant is the shape of the basal leaves. The lower leaves are reduced to a subulate petiole and are caducous. Later ones are sub-persistent, but always easily detached, with a slightly more pronounced short, blunt, linear-oblong blade. Other, less reliable, characters for identification are the rigid, slightly zigzag stem and the petals which have a cuneate base broadening upwards to a truncate top so that they appear to be distant from one another.

Cultivation experiments have shown that the morphology of the basal leaves remains unchanged when the plant is grown under terrestrial conditions; also that *R. flammula* subsp. *flammula* will not develop such leaves when grown in a few centimetres of water.

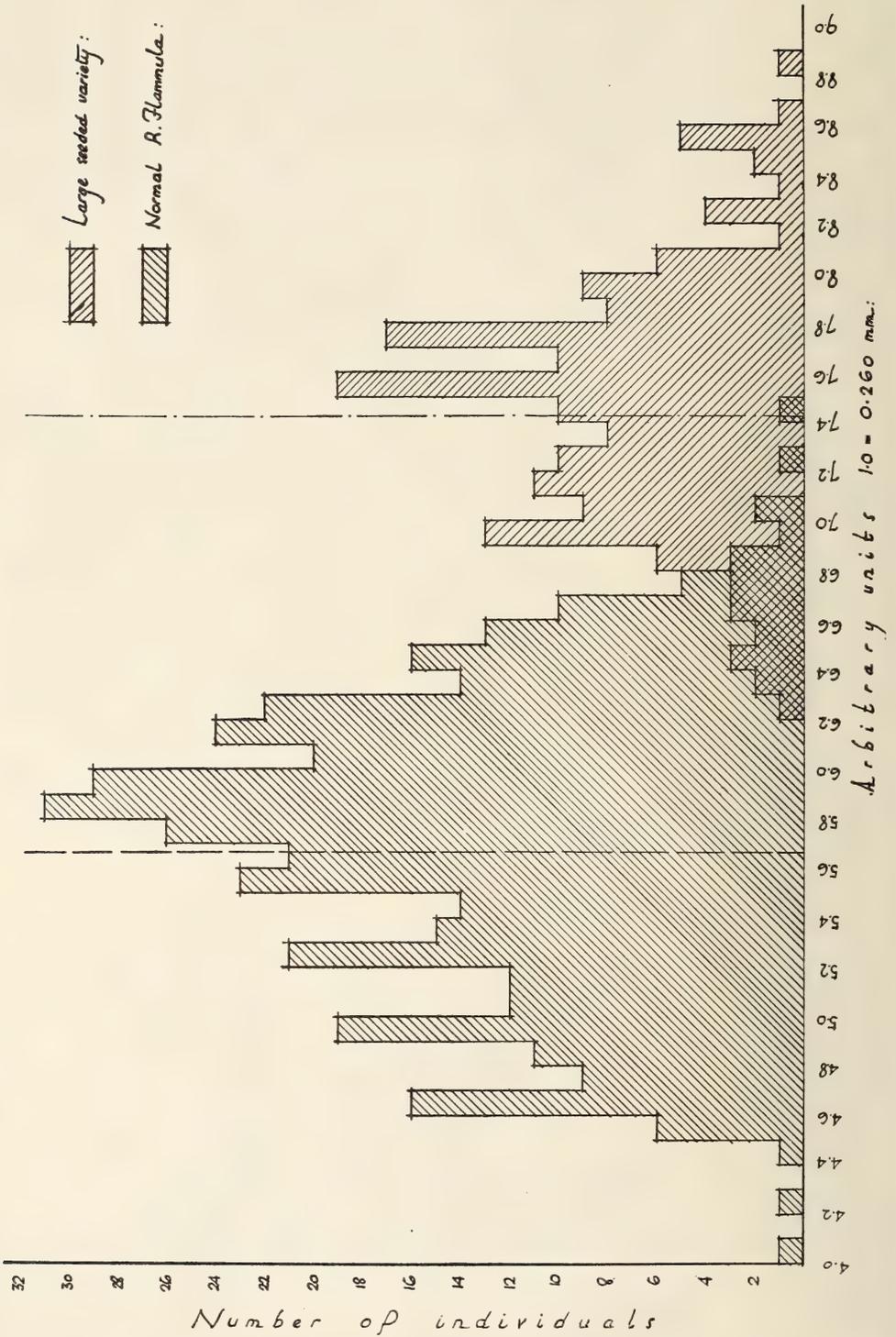


Fig. 4. Histogram of achene length in normal *R. flammula* and the variety from Orkney with large achenes.

There is therefore no doubt that this taxon is genetically distinct from *R. flammula*; it was reduced to a subspecies by Clapham (1952) and observations of plants both in the field and in cultivation indicate that this is probably the most appropriate category.

The distribution is difficult to determine from herbarium material, which rarely shows the basal leaves, since these usually drop off by the time flowering commences. It is, however, reasonably certain that it occurs in v.c. 98 (Argyll) and 104 (N. Ebudes) and also possibly H27 (W. Mayo); other records are probably erroneous.

RANUNCULUS REPTANS.

R. reptans is more common in Norway and Sweden than it is in the British Isles. Specimens from those two countries show a distinctive plant, extremely slender with arching internodes. Plants collected from the two best-known localities in Britain, Loch Leven and Ullswater, do not show such uniform morphology. Great variation in size and the degree of nodal rooting may be observed, the morphology varying according to the habitat. This variation has led to confusion with *R. flammula* 'forma *tenuifolius*,' and so, in an effort to establish a dividing line between the two, these localities were visited in 1952. The habitat in both was very similar. The plants occurring along the pebbly beach at the water line were very small and slender. Behind them, the plants became progressively stouter and less prostrate until, behind the high-water mark, there were populations of normal erect *R. flammula*. A representative selection of plants was brought into cultivation in June, 1952 and by the end of that growing season marked morphological changes could be seen in many of the plants. The most slender specimens which had been creeping along the water's edge remained prostrate; most of the intermediate forms, however, reverted to erect *R. flammula*, indicating that they should be assigned to *R. flammula* 'f. *tenuifolius*.' Clearly some method of distinguishing this form from *R. reptans* other than by cultural experiments was necessary and, in an attempt to discover some measurable characteristic, pollen grains were treated with lactophenol and cotton blue and examined. There were many shrunken and malformed grains and a survey was made to determine the percentage sterility. Using samples of not less than 300 grains from each plant it was found that the sterility varied from 10–90%. Values below 10% were not considered to be significantly subnormal. Although there was no absolute connection between percentage sterility and the type of morphology, nevertheless there was a distinct tendency for the more slender creeping plants to have the highest percentage sterility, while the closer the plants approached to *R. flammula* in their morphology the more fertile was the pollen. In no case was a plant of the slender type found to have fully fertile pollen (i.e. less than 10% sterile). These facts strongly suggest the possibility of introgressive hybridisation between *R. flammula* and *R. reptans* resulting in a hybrid swarm; the continual back-crossing with the most abundant species (*R. flammula*) having eliminated all genetically pure *R. reptans*.

Pollen from a collection of Swedish specimens was examined by the method described above, and it was found that in the north, where *R. flammula* is a great rarity, *R. reptans* had fully fertile pollen. Further south, however, the ranges of the two species overlap, and plants labelled *R. reptans* from this area showed varying degrees of sterility.

The only country from which *R. reptans* is reported, but where *R. flammula* is reputed to be absent, is Iceland. Herbarium material was obtained from Reykjavik and the pollen examined in the usual way; the majority of the plants were pure *R. reptans* with fully fertile pollen although there were a few specimens which were a rather dwarf semi-prostrate form of *R. flammula* which had been labelled *R. reptans* in error, probably owing to the fact they they showed a tendency to nodal rooting.

Although this cannot be regarded as conclusive proof, nevertheless it seems likely that the hypothesis of introgressive hybridisation is correct. It is probable that *R. reptans* was present in these islands in the Late-Glacial and that relict populations survived at Loch Leven and Ullswater and became modified at a later date by hybridisation and repeated back-crossing with *R. flammula*. If this is the case, it may be postulated that, so far as is known at the moment, there is no pure *R. reptans* remaining in the British Isles, and that the prostrate creeping forms to be found on northern lake shores are either:

- (a) *R. flammula* 'forma *tenuifolius*,' which will revert to normal *R. flammula* in cultivation, or (b) of hybrid origin.

As far as is at present known, these hybrids can only be certainly detected by examination of the pollen, which is more than 10% sterile.

SUMMARY

(a) Cultivation experiments and study of the literature have shown that the numerous described varieties of *R. flammula* may be reduced to the following taxa :—

- R. flammula* L.
 subsp. *flammula*
 var. *flammula*
 var. *major* Schult.
 subsp. *minimus* (A. Benn.) Padmore
 subsp. *scoticus* (E. S. Marshall) Clapham

(b) The hypothesis is put forward that, on account of introgressive hybridisation there is no genetically pure *R. reptans* remaining in the British Isles; it is suggested that the small creeping forms of the northern lake shores are either *R. flammula* 'forma *tenuifolius*' or of hybrid origin. In the latter case the pollen is always more than 10% sterile. Subsp. *flammula* is widespread and common in Britain as a plant of damp places. Subsp. *minimus* is a plant of northern sea coasts which has a very characteristic leaf shape. Subsp. *scoticus* grows in shallow water and has certain morphological characteristics which are retained in cultivation. It occurs in the Highlands of Scotland and possibly also in north-western Ireland.

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VARIATION IN *HELIANthemum canum* (L.) BAUMG. IN BRITAIN

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ABSTRACT

An account is given of variation in *Helianthemum canum* in the British Isles, based on both herbarium and cultivated material. There is significant variation in leaf-size and shape, leaf pubescence, and flower number, amongst other characters.

The British populations fall into three groups. The group most closely resembling neighbouring Continental populations comprises plants growing in lowland localities on Carboniferous Limestone near the coast of Wales and north-west England. A substantial proportion of the plants in all these populations have a felt of stellate hairs on the upper leaf surface.

The population on Cronkley Fell, in Teesdale, differs in its smaller and narrower leaves, which are subglabrous above, and always lack the stellate tomentum on the upper surface. The name 'var. *vineale* (Pers.)' is shown to be inapplicable to this plant, and subsp. *levigatum* subsp. nov. is proposed to replace it.

The Irish populations are characterised by coarse growth, large leaves, and more numerous flowers in the inflorescence. They are most closely approached by some Pyrenean plants.

The relation of the British plants to some Continental forms is discussed. In particular, it is concluded that the Teesdale plant is more closely related to the remaining British *H. canum* than to the Öland population with which some authors have united it.

INTRODUCTION

The genus *Helianthemum* is represented in central and northern Europe by *H. chamaecistus* and *H. apenninum*, and by the taxonomically complex aggregate of species including *H. canum*, *H. oelandicum* and *H. alpestre*. Of the latter group, *H. canum* is the only member reaching the British Isles. It is a very local plant in Britain, and here, as elsewhere on the edge of its area, its range is broken by a series of greater and lesser disjunctions (Fig. 1). Associated with these is marked inter-population variation. Each population tends to differ somewhat from every other, and the Teesdale population is distinct enough to have been commonly accorded taxonomic recognition as the 'var. *vineale*' of British authors. The variation of *H. canum* in Britain has attracted the attention of a number of botanists in the past, perhaps especially the late A. J. Wilmott. There are a number of herbarium sheets of *H. canum* collected and annotated by Wilmott in the British Museum herbarium and elsewhere, but his death in 1950 forestalled the publication of any conclusions.

Helianthemum canum has an equally disjunct distribution in other parts of central and northern Europe. In the south of Europe it has a more continuous area of distribution in calcareous montane grassland from north and east Spain (with southern outposts in Morocco and Algeria), through southern France, Italy, and the mountains of the Balkan Peninsula, to Asia Minor, and (taking the species in a broad sense) south Russia and the Caucasus. The most valuable taxonomic account of *H. canum* and its allies is the detailed and critical paper by Janchen (1907). Grosser's treatment of the group (Grosser, 1903) is

unsatisfactory, while the more recent monograph of the section *Chamaecistus* by Font Quer and Rothmaler (1934) is in some ways less modern in its approach to the paramorphs within *H. canum* than Janchen's earlier work. The *H. canum* group in the Soviet Union is treated in detail by Juzepczuk in *Flora U.R.S.S.* (Komarov, 1949). *H. canum* is disjunct

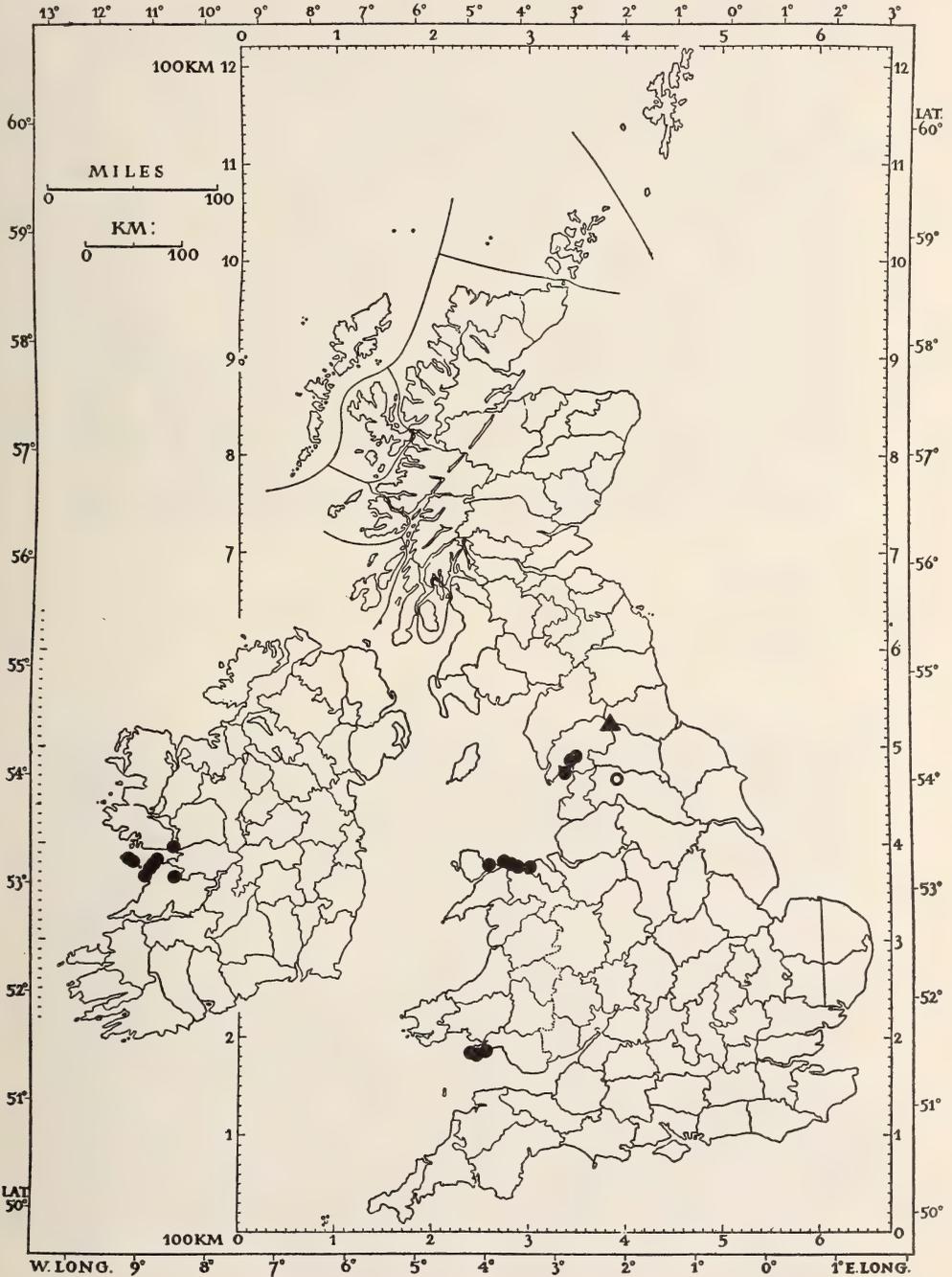


Fig. 1. Distribution of *Helianthemum canum* (L.) Baumg. in the British Isles. The Teesdale locality is indicated by the triangle. The open circle represents the Malham station, in which the plant has not been seen recently.

in S. Russia as it is in Britain, and shows a rather wider range of variation; and four paramorphs within the group are considered by Juzepczuk as distinct species.

The British *Helianthemum canum* populations fall into three groups: the Teesdale population, the western Irish populations, and the various populations on Carboniferous Limestone along the west coast of England and Wales. These three groups form not only convenient geographical units, but also recognisable taxonomic entities, which can be distinguished with fair certainty both in herbarium material and in cultivation. The lowland populations in Great Britain (Fig. 2, a & b; Plate 7, Fig. 1) vary a good deal amongst themselves, but on the whole they approximate most nearly to *H. canum* as it occurs on neighbouring parts of the Continent. Rather dense leaf pubescence is the rule, and their most striking feature is the occurrence of a proportion of individuals with a fine stellate felt over the upper leaf surface in addition to the usual more or less dense covering of coarser bristles. The Teesdale population (Fig. 2c; Plate 7, Fig. 2) is restricted to a few outcrops of metamorphic 'sugar limestone' near the summit of Cronkley Fell in N.W. Yorkshire. The site is bleak and exposed, and the plants are remarkably small-leaved and dwarf-growing amongst the closely cropped grass. The leaves are subglabrous or glabrous above, and never show any stellate tomentum on the upper surface. Plants from the limestone of the Burren district in the west of Ireland (Fig. 2, d & e) resemble the Teesdale population in the rare occurrence of stellate pubescence on the upper leaf surface. They differ from the Teesdale plant in their much larger and hairier leaves and coarser growth; differences which are obvious in the field and maintained in cultivation.

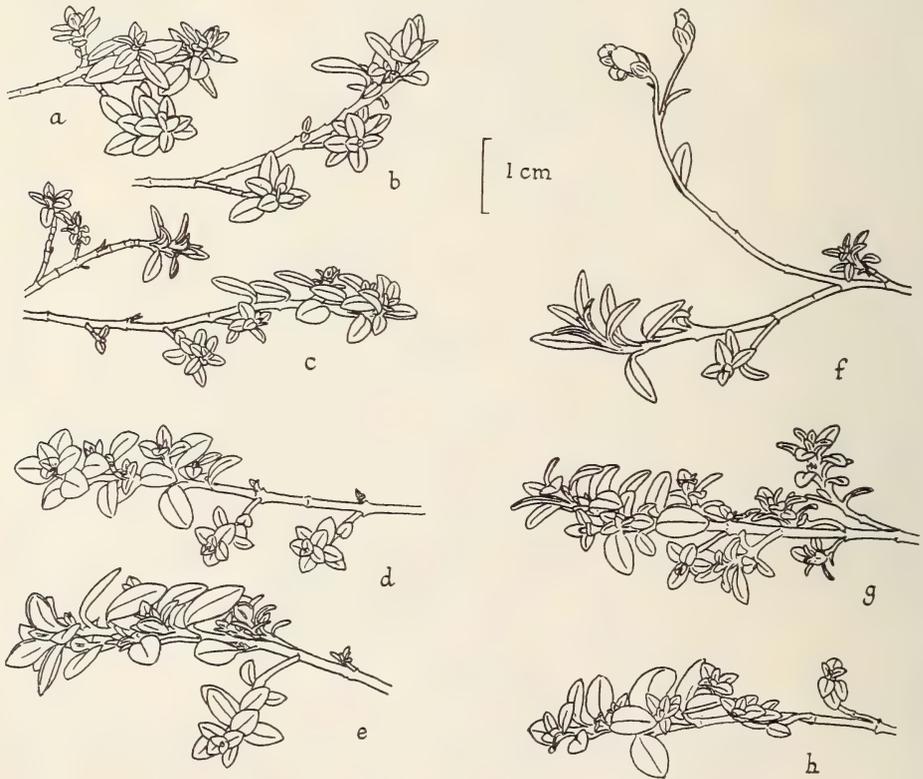


Fig. 2. Shoots of *Helianthemum canum* in cultivation, Oct. 1956. $\times 1$. a. Scout Scar. b. Humphrey Head. c. Teesdale. d. Black Head. e. Mullagh More. f. Södra Möckleby, Öland. g. Nüssenberg, nr. Laucha, Saxony. h. Cirque de Gavarnie, Htes. Pyrénées.

PLATE 7.



Fig. 1.

Helianthemum canum, Whitbarrow, Westmorland, 30 May 1952,
with *Festuca ovina*, *Sesleria caerulea*, *Galium pumilum*. (\times c. 2/3).



Fig. 2.

Helianthemum canum subsp. *levigatum*, Cronkley Fell, N.W. York., 27 May 1952,
with *Festuca ovina*, *Sesleria caerulea*, *Dryas octopetala*. (\times c. 2/3).



MATERIAL

During 1952-3 most of the important British localities for *H. canum* were visited, and material was collected, as plants, seeds, or cuttings, for cultivation on the experimental plot in Cambridge. Mature plants were not easy to establish, and seeds or cuttings proved much more satisfactory. The experimental plants from Teesdale and Ireland were rooted from cuttings in the summer of 1953, but other samples were grown from seed in spring 1954, and some older collections were also included. All the plants grew vigorously in their first season of growth following establishment, and there was little to choose between the two methods of propagation. In many characters plants in their second season remained reasonably comparable with the first year plants. After this, however, many of the older shoots died back, to be replaced by new growth from near the base, and the leaf size and general appearance of any individual plant depended greatly on the accidents of its previous history. In particular, many of the plants on the plot were damaged by the Phycomycete, *Peronospora leptoclada* Sacc., during the summer of 1955.

Collections of herbarium material were also made. Abundant material of *H. canum* from Teesdale and Great Ormes Head was available in Cambridge. The other localities were poorly represented, and the results given here are based on material of my own collection.

RESULTS

Leaf length and breadth were measured in both herbarium and cultivated material. Leaf size varies a great deal in each individual plant, so that the selection of the leaves to be measured is important. Almost all the herbarium material used was collected at or shortly after flowering time, and measurement of the longest leaves on the vegetative shoots proved reasonably satisfactory in practice. No attempt was made to use the leaves of the flowering shoots, as these appeared to show more chance variation amongst themselves and contributed less to the characteristic appearances of the different populations. Measurements on the cultivated material were made late in the summer of 1954. At this time the vegetative shoots which had developed in early summer had virtually finished their growth, and had given rise to many pinnately arranged lateral branches bearing most of the leaves. In general the longest of these late-summer leaves from each plant were taken for measurement, the few remaining coarse early-summer leaves being ignored.

Leaf length and breadth are not independent characters, but show a strong correlation. Length/breadth ratio is hardly a more constant character of a population than either character taken singly, and it too shows a strong correlation with length. Some interesting features emerge from a comparison of the results from herbarium specimens and cultivated material (see Fig. 3). In wild-collected material there is clearly a great deal of individual variation, and with the resulting overlapping most of the populations form a graded series from rather small-leaved plants at Humphrey Head and on the Gower coast to the longer and narrower-leaved plants in Ireland and in the inland localities in Westmorland. Only two extreme populations stand significantly apart; the very small- (and narrow-) leaved Teesdale population, and the large-leaved population at Mullagh More in Ireland.

In the cultivated plants a very much more distinct separation of the populations is seen (Fig. 4). In the wild material Teesdale provided the only exception to a very close correlation between leaf length and length/breadth ratio. Under cultivation this close correlation is obscured in the material as a whole, though it still remains distinct within each of the two larger population groups. The Teesdale plant is still the shortest-leaved and for their length the leaves show a relatively high length/breadth ratio. In both these characters it differs little more from the other populations in Great Britain than they differ

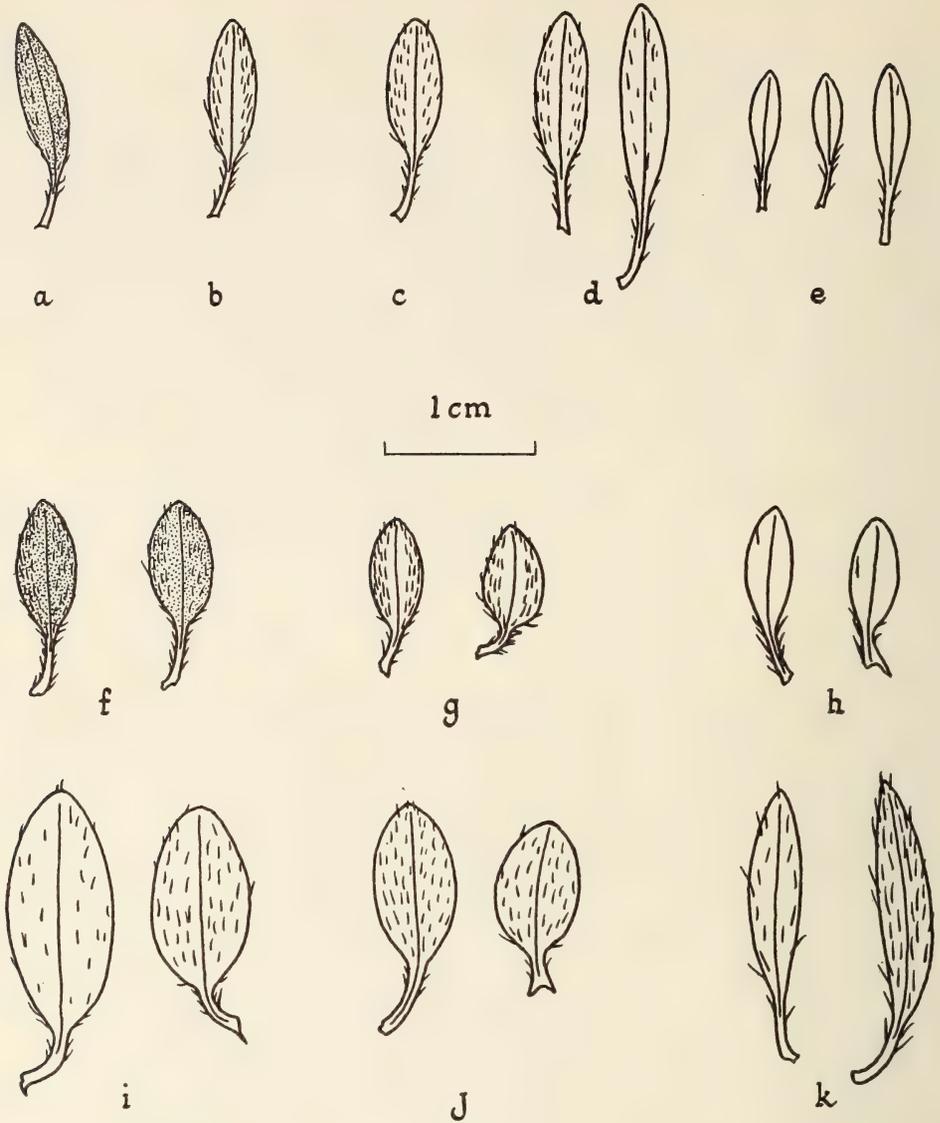


Fig. 3. Leaves of *Helianthemum canum* from British localities, $\times 2$. a. Whitbarrow. b. Great Ormes Head. c. Poulisallagh. d. Mullagh More. e. Teesdale. Leaves of *H. canum* in cultivation, $\times 2$. f. Humphrey Head. g. Rhossilli. h. Teesdale. i. Mullagh More. j. Black Head. k. Öland.

amongst themselves, but it is noteworthy that the Teesdale population lies off the almost linear trend of leaf variation of the other populations, which may be an indication that its distinctness from them is more far-reaching than their mutual differences.

The most striking results are provided by the Irish plants. In cultivation they became remarkably distinct from any of the other British populations, with coarse growth, and large broad leaves. Some botanists (e.g. Praeger, 1934) included the Irish plants at least tentatively with the Teesdale plant as 'var. *vineale*,' but it is clear that they are very different from it, and almost equally distinct from the lowland populations in Great Britain.

It is noticeable that plants from different populations do not necessarily show the same changes, or even parallel changes, on cultivation. Thus under wild conditions,

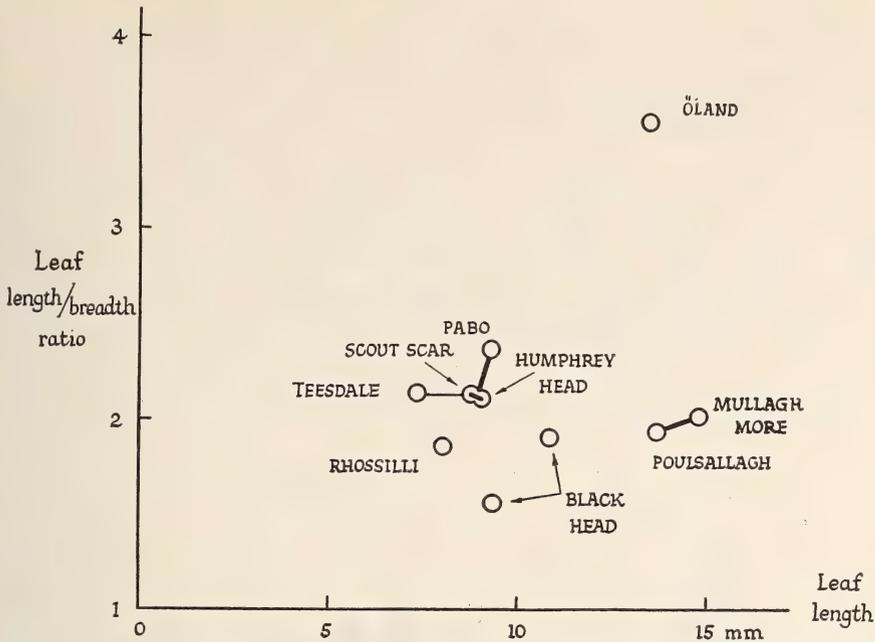


Fig. 4. Leaf size and shape in cultivated material of *H. canum*. Samples joined by thick lines do not differ at the 10% probability level in either length or length/breadth ratio (using Student's *t* distribution); those joined by a thin line differ in one or the other at the 10% but not at the 5% level. All other samples differ significantly at the 5% level in length, length/breadth ratio, or both.

plants from Humphrey Head are closely similar in leaf size and shape to plants from the Gower coast, and noticeably smaller than the Scout Scar population. In cultivation the Gower plants retain smaller and broader leaves than plants from Scout Scar; but the Humphrey Head and Scout Scar populations are now virtually indistinguishable in leaf size and shape, though they differ significantly from the Gower population. In other words, there is evidence that dwarfing in exposed maritime habitats is mostly purely phenotypic at Humphrey Head, but largely genetic in Gower. Similarly in the Irish populations, those on the west coast of the Burren are scarcely distinguishable in herbarium material, while the inland population at Mullagh More is distinctly larger-leaved. Cultivation shows that the Irish maritime populations are genetically heterogeneous, and that while the population in closed turf near Poulisallagh is potentially as large-leaved as that at Mullagh More, plants on the dry exposed slopes near Black Head constitute a definite small-leaved ecotype. A sample collected in closed turf below the road, a little to the south of Black Head, is intermediate between the two extremes. No doubt there exists a pattern of ecotypic adaptation to local habitat conditions. In the Gower population already mentioned the great exposure suffered by a large part of the population has apparently resulted in similar selection of a small-leaved ecotype; a process which has not occurred to any marked degree in the much smaller population under less severe conditions at Humphrey Head. It is interesting that in both these cases closely similar results are arrived at in different populations by ecotypic differentiation and by phenotypic plasticity. Clearly in an outbreeding species, such as this, strong ecotypic differentiation is unlikely to take place in response to small-scale and intricate habitat variation, and the variation pattern will reflect average conditions over rather broad areas. The Gower and North Wales populations of *H. canum* are extensive, and cultivation of further samples would probably show that they embrace within themselves much variation of this type.

Similar selection of a small-leaved form under conditions of extreme exposure is shown by the small Teesdale population. A particularly interesting feature here is the occurrence with *H. canum* of an exactly parallel and equally extreme form of *H. chamaecistus*. This has a closely prostrate habit of growth, small leaves almost or quite glabrous above, and short inflorescences; all characters which are kept in cultivation.

Leaf pubescence is a valuable character which changes little on cultivation. The pubescence comprises hairs of several types. The lower surface is thickly covered with a felt of long stellate hairs. The upper surface is more or less sparsely clothed with stiff and rather closely appressed bristles, generally in groups of several together. In addition, the upper surface is sometimes covered with a light stellate felt, giving the leaves a distinct grey appearance. Though the stellate tomentum varies in density, most plants show either a rather close covering of appressed stellate hairs or none at all. The distribution of pubescence of the upper surface in the material studied is summarised in Fig. 5.



Fig. 5. Distribution of leaf pubescence characters in British populations of *Helianthemum canum* (from herbarium material). Ordinates are percentage frequencies. The bristle classes represent roughly: 1, almost or quite glabrous; 2, c. 10-12 bristles on leaf; 3, c. 25 bristles on leaf; 4, c. 50 bristles on leaf or c. 10 on a square area from midrib to margin; 5, very dense, covering c. 1/5 area of leaf or more.

As would be expected, the Teesdale plant stands out with its generally sparse pubescence, and the rather hairier Irish plants are also clearly separated from the remaining populations. In these, the stellate pubescence seems to occur in a much higher proportion of plants in Westmorland than in North Wales or Gower. Any more detailed examination of its distribution would require more material than was used in the present study, and the sampling technique would need to be carefully devised to avoid bias in sampling for such a conspicuous character. Janchen (1907) found similar variation in most of the Continental populations he studied; stellate-pubescent plants were abundant in some but

rare or absent in others. Field observation in this country suggests that where they occur plants with stellate pubescence tend to predominate in the driest rocky areas, and to be sparse in the moister areas of closed turf; a conclusion consistent with Janchen's observations. The question merits more attention, particularly in relation to the differentiation of the Irish and Teesdale populations.

The number of flowers in the inflorescence is a character of some weight in the *H. canum* group. It is not an easy character to use unless ample material is available, as it depends to some degree on environment, and shows a wide variation even on an individual plant (Fig. 6). In general, flower number tends to increase from north to south in Europe, but there is much local variation. The mean flower numbers for some

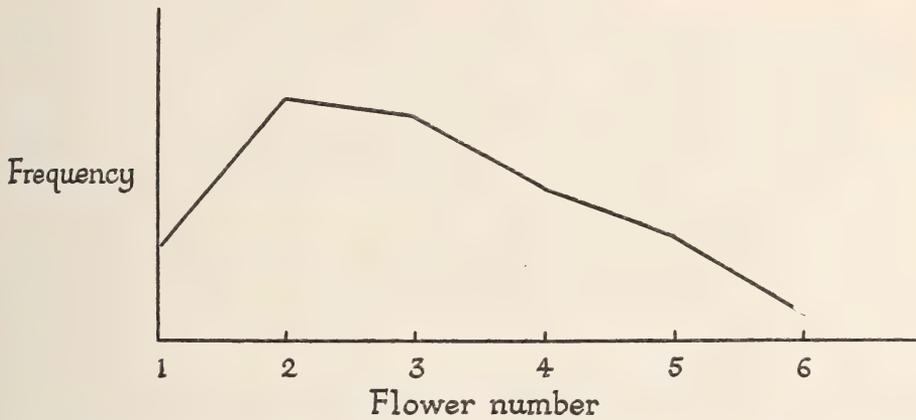


Fig. 6. Distribution of flower number in a wild population of *Helianthemum canum*; Whitbarrow, May 1952. 167 inflorescences counted; mean number of flowers/inflorescence 3.02.

of the British plants cultivated are given in Table I, together with figures for some Continental plants for comparison. A hundred or more inflorescences were counted in each case, a complete sector of the plant being stripped from the centre to the edge. The figures are probably all somewhat too low, as the counts were made at the end of the flowering period, and a proportion of flowers which dropped off, having failed to set seed, must have been missed.

The most striking result which emerges from this table is the high flower number (and inflorescence length) of the Irish plant. It is most nearly approached in flower number by the population from the Cirque de Gavarnie in the Pyrenees, but exceeds this by a

TABLE I.

Flower number and inflorescence height in cultivated material of *Helianthemum canum*. Flower numbers are means from 100 or more inflorescences; heights are means of 10 measurements.

Locality	Mean flower number	Inflorescence height (c.m.)
Scout Scar	4.04	6.7
Teesdale	3.30	6.1
Teesdale (1952)	3.75	—
Black Head	4.91	10.8
Cirque de Gavarnie	4.35	9.0
St. Adrien, nr. Rouen	3.27	—
Nüßenberg, Saxony	2.58	9.0

substantial margin. Data are not available for a comparable series of plants from all the British localities, but it seems that in most other cases the mean flower number must lie between about 3 and 4.5.

The figures from herbarium material in Table II show a similar trend, but all the figures, and especially those for Teesdale and North Wales, are probably biased by the natural tendency to collect conspicuous or well-grown specimens.

TABLE II.
Mean flower number in herbarium material of *Helianthemum canum* from British localities.

Locality	Mean fl. number	Infls. counted	Standard deviation
Westmorland	3.61	118	1.37
Teesdale	2.71	52	0.73
N. Wales	4.30	130	1.33
Ireland	5.22	155	1.88

DESCRIPTIONS OF BRITISH FORMS OF *H. CANUM*

It will be useful at this point to summarise the main features of the British *H. canum* populations.

(a) *Wales and N.W. England*

The plants from these populations are the most like those from the neighbouring parts of the Continent, and probably transgress little outside the Continental range of variation. They are variable in habit, but form more or less compact mats of prostrate shoots, less coarse in growth than the Irish plants, and less strictly prostrate than the Teesdale population. Leaves rather short (the longest c. 6-10 mm.; 7-11 mm. in cultivation), shortly petioled; more or less densely hairy with the abundant long bristles on the upper surfaces. In addition, a substantial but variable proportion of individuals in all the populations have a light or dense covering of short stellate hairs on the upper leaf surface. Inflorescence c. 6-8 cm., most commonly 2-5-flowered. Buds globose, c. 3 mm. long, sepals stellate-pubescent and pilose; petals c. 5-7 mm. Flowering pedicels erect to spreading, often slightly deflexed after flowering, and more or less spreading in fruit.

The leaves form rather condensed rosettes towards the stem apices in late summer and autumn. In this feature there is a range of variation between the continental central European populations, with a marked and almost bud-like forward-facing autumn rosette of leaves separated only by very short internodes, and the populations in oceanic parts of western Europe in which broad flat leaves persist well down the stem and the apical rosette is scarcely noticeable. The English and Welsh plants, with the flattish upward-facing rosettes, occupy an intermediate position in this range. They are not usually vigorous plants in cultivation, often forming a smaller or looser mat of vegetative growth than the Teesdale plant and seldom very much larger; and they seem more prone to dying back during the winter than the other British plants.

(b) *Teesdale* (Fig. 2c; Fig. 3 e & h; Plate 7, Fig. 2)

Differs from the lowland English and Welsh plants most strikingly in its small leaves which are glabrous or subglabrous above, and varies little. Habit closely prostrate, forming a flat intricately branched mat tightly appressed to the ground. Leaves small (the longest c. 6 mm. \times 2 mm.; c. 8 mm. \times 3.5 mm. in cultivation), thick, subacute or

subobtuse, and slightly revolute at the margin, dark green and almost or quite glabrous above, densely stellate-tomentose below, with a shortish to rather long petiole. Inflorescence short (c. 3-6 cm.), most commonly 1-3-flowered (c. 2-5-flowered in cultivation). Buds globose, c. 3 mm. long, sepals stellate-tomentose and lightly pilose, petals c. 5-6 mm.

The Teesdale plant is very distinct from the other British forms of *H. canum* in cultivation, and in the field the phenotypic expression of its distinctive features is intensified by the bleak habitat. The leaves form distinct apical rosettes in autumn; and in this respect the Teesdale plant more closely resembles central European forms than do any of the remaining British *H. canum* populations.

(c) *Ireland* (Fig. 2 d & e; Fig. 3 c, d, i, & j)

Coarser in growth than the other British forms, forming dense spreading mats of prostrate shoots. Leaves large (c. 7-12 mm. \times 2-4 mm.; 9-15 mm. \times 5-7 mm. or more in cultivation), subacute to obtuse, flat or slightly revolute at the margin, green and sparsely hairy above (rarely lightly stellate-tomentose), densely stellate-tomentose below, with a shortish to rather long petiole. Inflorescence tall (c. 6-10 cm.), most commonly 4-6-flowered, sometimes branched. Buds globose, c. 4 mm. long, sepals stellate-tomentose and pilose, petals c. 5-7 mm.

In the field Irish plants may differ little in leaf size from those from the west coast localities in Great Britain, but they usually differ obviously in their sparsely hairy and often rather long-petioled leaves. Their noticeably long winter internodes may be attributed at least in part to the direct influence of the western Irish climate; though in cultivation (and apparently also in the field) they form the least distinct winter rosettes of any of the British forms, the large flat leaves persisting well down the stem throughout the winter.

DISCUSSION

The group including *H. canum* and the *H. alpestre*-*H. oelandicum* aggregate is an intricate one, and has suffered much taxonomic and nomenclatural confusion. In Britain this has involved mainly the Teesdale plant. Syme (1873) says, "I am indebted to Mr. J. G. Baker for pointing out to me that the Teesdale plant is *H. vineale* Pers.", and the plant has been widely known to British botanists by this name.

The original description of *Cistus vinealis* by Willdenow (1799) is as follows:

"*Cistus vinealis* W.

C. suffruticosus procumbens exstipulatus, foliis petiolatis oblongis obtusis subtus incano-tomentosis, floribus racemosis."

Though this description disagrees in no way with the Teesdale plant (except perhaps "foliis . . . obtusis"), it agrees equally well with other forms of *H. canum*, and Willdenow clearly intended it to apply to the populations "in Germaniae vineis, inque Helvetia." These are in most respects more closely comparable with the plants of the lowland limestone areas in Great Britain than with the Teesdale plant (cf. material cultivated from Saxony, Fig. 2g). Persoon (1805) repeats Willdenow's description and gives the same localities. Thus the name *H. canum* var. *vineale* (Pers.) cannot be used in a restricted sense for the Teesdale population.

Janchen (1907) included in "*H. canum* f. *vineale* (Willd.) Syme & Sowerby" all the central and west European forms, with the exception of the Teesdale and Öland plants, and the diverse forms in the south of France and the Iberian peninsula. Janchen agreed with Willkomm (1856) and Grosser (1903) in uniting the Teesdale and Öland plants, though he used Hartman's name *canescens* (1820, as var.) rather than Willkomm's later

name *microphyllum* (1856, as var.). Like Grosser, he placed them under *H. oelandicum*, as a variety of which the Öland form was originally described.

Fortunately, through the kindness of Dr. R. Sterner, I have been able to cultivate several samples of *H. canum* from Öland, which have shown conclusively that the Öland form is quite distinct from the Teesdale plant. Apart from its marked differences in leaf size and shape (Fig. 2f; Fig. 3k; Fig. 4) and hairier leaves, it has a looser habit, and flowers continuously throughout the latter part of the summer (as noted by Sterner, 1936). In this last feature it differs not only from all the British populations, but also from material cultivated from Saxony, the Seine valley, and the Pyrenees; though similar flowering on the current season's shoots during the latter part of the summer certainly occurs and is probably widespread in south Europe.

The Teesdale population lies much closer in all its characters except leaf pubescence to the more widespread lowland forms in Great Britain; that is, it belongs to Janchen's *H. canum* f. *vineale* rather than to his *H. oelandicum* f. *canescens*, the latter name belonging properly to the Öland plant. It remains to consider Willkomm's very appropriate epithet *microphyllum* (1856, as var.). Willkomm included three plants under this: the Öland plant (for which the earlier epithet *canescens* Hartman (1820, as var.) is available, the Teesdale plant, and a plant from N. Spain. No indication is given in the description which was regarded as the type form, but the Spanish plant is figured. Further, Font Quer & Rothmaler (1934) and Guinea (1954) have used this epithet (the former as *H. canum* var. *canescens* f. *microphyllum* (Willk.) F.Q. & Rothm. and the latter as *H. canum* var. *microphyllum* (Willk.) Guinea) for north Spanish taxa, which neither include nor closely resemble the Teesdale plant. Thus it appears that there is no name available for the Teesdale form, though it is certainly distinct enough to merit some recognition. Sub-specific rank appears the most appropriate for a geographical variant of this kind, and the name *H. canum* subsp. *levigatum* is proposed for it.

***Helianthemum canum* subsp. *levigatum* Proctor subsp. nov.**

Habitus perprostratus, ramis multis ad terram adpressis. Folia crassa, parva, longissima, c. 6 mm. × 2 mm. (in horto c. 8 mm. × 3.5 mm.), angusta subobtusata vel subacuta, supra viridia subglabra vel glabra semper sine pilis stellatis, subtus stellato-tomentosa, margine leviter revoluta. Inflorescentia humilis (c. 3-6 cm.; in horto c. 6-8 cm.), vulgatissime 1-3-flora (in horto 2-5-flora). Alabastra globosa, c. 3 mm. longa; sepala stellato-tomentosa et leviter pilosa; petala c. 5-6 mm. longa. Habitat in pascuis siccis in 'sugar limestone' prope summum Cronkley Fell, Teesdale, Yorkshire.

Holotypus in Herb. Univ. Cantab. : v.c. 65, N.W. York; Cronkley Fell, Upper Teesdale, E. S. Marshall, 2 July, 1886.

The Teesdale plant is well represented in all the more important British herbaria, so it is unnecessary to cite further specimens.

It has been shown that the Irish plants are very clearly distinct from the other British populations. They are less strikingly distinct when they are compared with a series of Continental forms. Thus a plant in cultivation from the chalk cliffs of the Seine valley south of Rouen was somewhat intermediate in leaf characters between plants from Carboniferous Limestone in Great Britain and in Ireland, though it scarcely approached the Irish plants in coarseness of habit. The Pyrenean population cultivated (which appeared to agree most closely with *H. canum* f. *piloselloides* (Lap.) Janchen) was the most like the Irish plants in general appearance, resembling them particularly in the rather flat leaves, and the tendency of the lower leaves on the shoots to persist into the autumn and winter. Janchen's comment, that the leaves of his west Pyrenean and north Spanish

f. alpinum (Willk.) Gross. are green or lightly tomentose above, is perhaps significant in this connection. The resemblance is an interesting one, suggesting a parallel with a 'Lusitanian' distribution like that of *Saxifraga hirsuta*, but it may reflect simply the selection of similar forms in response to somewhat comparable habitat conditions. The Irish plants differed in their larger and less hairy leaves, coarser habit, and longer inflorescences. They are possibly distinct enough from any Continental form to be worth recognition as an independent subspecies. However, they are undoubtedly close to at least some populations of *f. piloselloides* (Lap.) Janchen and *f. cantabricum* F.Q. & Rothm., and without a more detailed knowledge of the variation in these it would be premature to separate them, though further study may show that separation is both practicable and desirable.

DISTRIBUTION OF *H. CANUM* IN THE BRITISH ISLES

In the following list no date or collector is given where I have seen the plant in a locality in the course of the present work. In all other cases the source of the information is quoted. National Grid references are added in brackets.

- V.c. 41. GLAMORGAN : (information largely from M. E. Griffiths, unpub.) Worm's Head (SS/393876); N.W. facing cliffs from Rhossilli (c. SS/409880) to Worm's Head, and S. facing cliffs from Worm's Head to Port Eynon (SS/468843); cliffs S. of Oxwich (c. SS/487856-512850); cliffs S. of Pennard, eastwards to Pwll Du Head (c. SS/540878-572863); cliffs between Caswell Bay and Langland Bay (c. SS/597870-605870).
42. BRECON : Trow (1911) gives a record for "Merthyr Tydfil": the main limestone outcrops on which the plant might occur are in Breconshire. A specimen in the University Herbarium at Oxford is labelled "Brecon, May 1859." (Both records are probably errors.)
49. CAERNARVON : Great Ormes Head (SH/750840-780830); Bryn Maelgwyn, Gloddaeth (SH/795805), and scattered from here to Little Ormes Head (SH/817828); near Pydew and Pabo (c. SH/810790).
50. DENBIGH : Bryn Euryn (SH/832798); Tan Penmaen Head (SH/880787); S. of Llysfæen (SH/888733; 895766; 900765) Cefn-yr-Ogof, Llanddulas (SH/914776).
51. FLINT : Craig Fawr, Meliden (SJ/059804); Moel Hiraddug, Dyserth (SJ/064782); W. side of Gop Hill, Newmarket (Dallman, 1911a) (c. SJ/084801).
52. ANGLESEY : Bwrdd Arthur (SH/585813); Mariandyrus (Griffith, 1894) (c. SH/600810).
64. M.W. YORK : Malham Cove (Lees, 1888) (SD/897641). A specimen collected by Lees in July 1880 is in Herb. Mus. Brit.; it is a rather small-leaved plant (longest leaves c. 7.5 mm. × 2.2 mm.), densely hairy but without stellate pubescence on the upper leaf-surface. It is evidently of the normal lowland type, and much like some material from v.c. 69. The plant has not been seen here since.
65. N.W. YORK : Cronkley Fell, Teesdale (NY/841283-845284).
69. WESTMORLAND : Underbarrow Scar (Scout Scar) from Brigsteer to the road west of Kendal (SD/485895-486924); south and west sides of Whitbarrow (c. SD/457851-438870); Humphrey Head (SD/392735).
- H9. CLARE : West Coast of Burren from Black Head south to Poulsallagh; cliffs of Moher (Praeger, 1934); Mullagh More, N.E. of Corrofin; Aran Islands (Praeger, 1934, &c).
- H16. GALWAY : Salthill, nr. Galway (Praeger, 1934).

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SOME NEW NAMES IN THE BRITISH FLORA

Dryopteris lanceolatocristata (Hoffm.) Alston, comb. nov. *Polypodium filix-femina* var. *spinosa* Weis, 1770, *Pl. Crypt. Fl. Gotting.*, 316. *P. spinulosum* O. F. Muell., 1777, *Fl. Dan.*, 4 (12), 5, excl. t. 707; non *P. spinulosum* Burm. f., 1768. *P. spinosum* (Weis) Schrank, 1789, *Baier. Fl.*, 2, 424; non *P. spinosum* L., 1753. *P. lanceolatocristatum* Hoffm., 1790, in Roem. & Usteri, *Bot. Mag.*, 3 (9), 9. *Aspidium spinulosum* Sw., 1801, in Schrad., *J. Bot.*, 1800 (2), 38 (nom. illegit.). *Nephrodium spinulosum* Strempel, 1822, *Fil. Berol. Syn.*, 30 (nom. illegit.). *Lastrea spinulosa* C. Presl, 1836, *Tent. Pterid.*, 76 (nom. illegit.). *Dryopteris spinulosa* Watt, 1866, *Canad. Naturalist*, new ser., 3, 159 (nom. illegit.); E. F. Warb., 1952, in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 40.

The name *Polypodium spinulosum* O. F. Muell. must be rejected as a later homonym of *P. spinulosum* Burm. f., which is *Synaphea spinulosa* (Burm. f.) Merr. in the Proteaceae (cf. Merrill, 1919, *Proc. Linn. Soc. New S. Wales*, 44, 353-354). O. F. Mueller's plate 707 in the *Flora Danica* was identified by Woyнар (1918, *Österr. Bot. Zeitschr.*, 67, 268) as *Dryopteris uliginosa* (Newm.) Kuntze ex Druce, but it cannot be regarded as the type of Mueller's *Polypodium spinulosum* which in fact is based on a plant figured and described, but not named, by him in 1767, *Fl. Fridrichsdal.*, 193, fig. 2. Maxon (1921, *Proc. Biol. Soc. Wash.*, 34, 111) drew attention to Watt's paper in which the transfer of Mueller's species to *Dryopteris* was made.

The next earliest specific name is *Polypodium spinosum* (Weis) Schrank, but this also is a later homonym and must be rejected. The earliest legitimate specific name appears to be *P. lanceolatocristatum* Hoffm., based on a fern probably from near Erlangen in Bavaria.

A. H. G. ALSTON

Ophioglossum vulgatum subsp. **ambiguum** (Coss. & Germ.) E. F. Warb., comb. nov. *O. vulgatum* var. *ambiguum* Coss. & Germ., 1861, *Fl. Env. Par.*, ed. 2, 874. *O. polyphyllum* auct.; non A. Braun, 1844. *O. vulgatum* subsp. *polyphyllum* E. F. Warb., 1952, in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 54, pro parte, excl. syn. A. Br.

Pichi-Sermolli (1954, *Webbia*, 9, 632-641) has shown that *O. polyphyllum* A. Braun is a different species from the European and Azorean plant which has been called by that name. If the latter is regarded as a subspecies of *O. vulgatum* a new combination is necessary. Fuller synonymy of both taxa will be found in Pichi-Sermolli's paper.

E. F. WARBURG

RHYNCHOSINAPIS Hayek, 1911, *Beih. Bot. Centralbl.*, 27 (1), 260, t. 10 fig. 32. *Brassicella* Fourr. [1868, *Ann. Soc. Linn. Lyon*, nouv. sér., 16, 330 (nom. nud.)] ex O. E. Schulz, 1916, in Engler, *Bot. Jahrb.*, 54, Beibl. 119, 52 (nom. illegit.).

The name *Brassicella* was originally published by Fourreau in 1868 as a *nomen nudum*. It was adopted by O. E. Schulz in 1916, but in the meantime the name *Rhynchosinapis* had been legitimately published by Hayek. Two species, *R. monensis* (L.) Dandy and *R. wrightii* (O. E. Schulz) Dandy, are recognised as native in Britain. A third, occurring as an alien and established in various places, requires a new combination, as follows.

Rhynchosinapis cheiranthos (Vill.) Dandy, comb. nov. *Brassica cheiranthos* Vill., 1779, *Prosp. Pl. Delph.*, 40. *Sinapis cheiranthos* (Vill.) Koch, 1833, in Röhl., *Deutsch. Fl.*, 4, 717. *Brassicella cheiranthos* (Vill.) Fourr., 1868, *Ann. Soc. Linn. Lyon*, nouv. sér., 16, 330

(comb. illegit.); Pugsley, 1936, *J. Bot.*, **74**, 326. *B. erucastrum* O. E. Schulz, 1916, in Engler, *Bot. Jahrb.*, **54**, Beibl. 119, 53, pro parte, excl. syn. L. *Rhynchosinapis erucastrum* Dandy, 1952, in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 158, pro parte, excl. syn. L.

The combination *R. erucastrum*, applied to this species in 1952, was published through a misunderstanding, *R. cheiranthos* being intended. I agree with Pugsley (loc. cit., 325) that it is not easy to see any valid ground for substituting the epithet *erucastrum* for *cheiranthos* as was done by O. E. Schulz.

J. E. DANDY

Tuberaria guttata subsp. ***breweri*** (Planch.) E. F. Warb., comb. nov. *Helianthemum breweri* Planch., 1844, in Hook., *Lond. J. Bot.*, **3**, 618, t. 21. *Tuberaria breweri* (Planch.) Willk., 1859, *Icon. & Descr. Pl.*, **2**, 77. *Helianthemum guttatum* subsp. *breweri* (Planch.) Syme, 1865, *Engl. Bot.*, ed. 3, **2**, 8, t. 166; E. F. Warb., 1952, in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 264. *H. guttatum* var. *breweri* (Planch.) Bab., 1874, *Man. Brit. Bot.*, ed. 7, 38. *Tuberaria guttata* var. *breweri* (Planch.) Grosser, 1903, in Engler, *Pflanzenr.*, **IV**, **193**, 57.

E. F. WARBURG

Kohlrauschia Kunth, 1838, *Fl. Berol. Fam. Nat. Dispos.*, **1**, 108. *Imperatia* Moench, 1794, *Meth. Pl.*, 60; non *Imperata* Cyr., 1792. *Tunica* sensu Pax & Hoffm., 1934, in Engler & Prantl, *Nat. Pflanzenfam.*, ed. 2, **16c**, 355.

The name *Tunica*, used for this genus by Pax and Hoffmann and by many other authors, is not applicable. It was first published by Ludwig (1757, *Inst. Reg. Veg.*, ed. 2, 129) as an illegitimate substitute for *Dianthus* L.; and it was also used in place of *Dianthus* by Haller (1768, *Hist. Stirp.*, **1**, 391) and Scopoli (1772, *Fl. Carniol.*, ed. 2, **1**, 298). The earliest name for Pax and Hoffmann's genus is *Imperatia* Moench, but this is a later homonym of *Imperata* Cyr. *Petrorhagia* Link (1831, *Handb. Erkenn. Gewächse*, **2**, 235), correctly cited "e.p." by Pax and Hoffman, is based implicitly on *Gypsophila* sect. *Petrorhagia* Ser. (1824, in DC., *Prodr.*, **1**, 354), the same species being included, and is to be typified by *Gypsophila glomerata* Pall., Seringe's first species and the one best agreeing with his definition of the section. Thus *Petrorhagia* is a synonym of *Gypsophila* L. and not of *Tunica* as delimited by Pax and Hoffmann, and the correct name for this latter genus is *Kohlrauschia* Kunth.

K. prolifera (L.) Kunth is native in southern Britain and the Channel Islands. The following alien species is established at Tenby in Pembrokeshire.

Kohlrauschia saxifraga (L.) Dandy, comb. nov. *Dianthus saxifragus* L., 1753, *Sp. Pl.*, 413. *Gypsophila saxifraga* (L.) L., 1759, *Syst. Nat.*, ed. 10, **2**, 1028. *Tunica saxifraga* (L.) Scop., 1772, *Fl. Carniol.*, ed. 2, **1**, 300. *Petrorhagia saxifraga* (L.) Link, 1831, *Handb. Erkenn. Gewächse*, **2**, 235.

J. E. DANDY

Herniaria ciliolata Melderis, nom. nov. *H. ciliata* Bab., 1836, *Trans. Linn. Soc. Lond.*, **17**, 453; Syme, 1867, *Engl. Bot.*, ed. 3, **7**, 179, t. 1172; Butcher & Strudwick, 1930, *Furth. Ill. Brit. Pl.*, 281, fig. 299; Clapham, 1952, in Clapham, Tutin & Warburg, *Fl. Brit. Is.*, 333, fig. 32A; non *H. ciliata* Clairv., 1811.

This taxon was originally described by Babington from Cornish (Lizard Point) specimens under the name *H. ciliata*. Unfortunately, his specific name is invalidated by an earlier homonym, and therefore the above new name is proposed.

Babington's species was reduced by Daveau (1893, *Bol. Soc. Brot.*, **10**, 95) to a variety of *H. maritima* Link, a species based on Portuguese specimens from Fort St. Julian. Sampaio (1947, *Fl. Portug.*, 338) transferred Babington's species as a variety to *H. vulgaris* Hill, which has been considered synonymous with *H. glabra* L. A close comparison of

H. ciliolata, on the one hand, with *H. maritima* and *H. glabra*, on the other, shows that it is more closely allied to *H. maritima* than to *H. glabra*. Both *H. ciliolata* and *H. maritima* are evergreen dwarf shrubs with shoots which are usually pubescent on only the upper side and are woody towards the base, while *H. glabra* is an annual or biennial with usually herbaceous shoots which are pubescent all round. The stipules in *H. ciliolata* and *H. maritima* are up to 2 mm. long, broadly ovate-acuminate, while those in *H. glabra* are smaller, inconspicuous and ovate. The sepals in *H. ciliolata* and *H. maritima* are about 1 mm. long; again *H. glabra* is distinguished from both in having smaller flowers, with sepals only 0.5–0.6 mm. long. The fruit in *H. ciliolata* and *H. maritima* is obtuse above, about equalling the sepals, while *H. glabra* has an acute fruit, considerably exceeding the sepals. Although *H. ciliolata* has many characters in common with *H. maritima* it is itself a distinct taxon. *H. maritima* differs from *H. ciliolata* in having a more robust stature; its stem is rugose, prominently noded, thicker and more hairy; the leaves are more rounded and fleshy, furnished with bristles not only on the margin, but also on both surfaces (in *H. ciliolata* they are glabrous on both surfaces and more or less ciliate on the margin). The stipules in *H. maritima* are greenish as in *H. glabra* while those in *H. ciliolata* are white. The sepals of *H. maritima* bear spreading bristles on the whole outer surface, while those in *H. ciliolata* are glabrous on the outer surface, often tipped with a deciduous bristle and in the typical plant usually glabrous on the margin.

H. ciliolata is a rare plant in Britain, occurring on maritime sands and rocks in Guernsey and W. Cornwall (Lizard Point). In Jersey it is represented by var. **angustifolia** (Pugs.) Melderis, comb. nov. (*H. ciliolata* var. *angustifolia* Pugs., 1914, *J. Bot.*, **52**, 331). This variety differs from the typical one by having smaller, narrowly elliptic leaves and sepals ciliate on the margin.

Outside Britain *H. ciliolata* is reported to be distributed on coasts of W. and N.W. Europe from Portugal to N. Germany. Continental material shows quite a wide range of variation. A critical revision, based on cytological evidence, genetical experiments and cultivation of biotypes under uniform conditions, is much needed. As regards the cytological data known at present, British plants of *H. ciliolata* (from Guernsey and W. Cornwall) are characterised by having a chromosome number $2n = 72$, while of Portuguese plants referred to *H. maritima* var. *ciliolata* two chromosome-races with $2n = 108$ and 126 have been discovered (cf. Blackburn & Adams, 1955, *Proc. B.S.B.I.*, **1**, 380).

A. MELDERIS.

Sorbus pseudofennica E. F. Warb. [1952, in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 546, fig. 42c (sine diagn. lat.)], sp. nov. A *S. hybrida* L. differt foliis minoribus supra magis flavescens, subtus minus tomentosis et minus albis, floribus multo minoribus, fructu longiore quam lato.

Arbor parva gracilis. *Folia* 5.5–8.5 cm. longa, oblonga vel obovato-oblonga, (1.3–) 1.5–1.7 (–2.2)-plo longiora quam lata, saepissime 1 (–2) paribus foliolorum basi praedita sed nonnunquam sine foliolis liberis, apicem versus lobata, praecipue loborum apices versus serrata, apice lato acuta obtusave, matura supra obscure lutescenti-viridia glabra, subtus subtenuiter cinereo-tomentosa; nervi utrinque 7–9 (–10); petiolus 8–20 mm. longus. *Petala* c. 4 mm. longa. *Antherae* albae. *Fructus* 7–10 mm. longus, longior quam latus, scarlatinus, lenticellis paucis parvis praeditus.

Holotypus in Herb. Mus. Brit.: v.c. 100, Clyde Is., Arran, Glen Catacol, E. F. Warburg (no. 224), September 1937.

This is the Arran plant to which the name *S. hybrida* or *S. fennica* has been applied. Glen Catacol is the only locality known.

Sorbus leptophylla E. F. Warb. [1952, in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 550, fig. 43K (sine diagn. lat.)], sp. nov. A *S. aria* (L.) Crantz differt marginibus foliorum apicem et basin versus rectis ut partes apicales basalesque foliorum triangulares sint, foliis subtus magis tenuiter tomentosus, dentibus crassioribus et paucioribus, dente apicali et eis nervos primarios terminantibus dentes ceteros multo excedentibus, fructu semper lenticellis mediocribus parvisque subpaucis praedito.

Arbuscula. *Folia* saepissime obovata, (8-) 9-12 (-14) cm. longa, (1.3-) 1.5-1.7 (-2.5)-plo longiora quam lata, apice acuta, basi cuneata, marginibus apicem et basin versus per tertiam partem folii rectis, tenuia, sub fructu supra lutescenti-vel obscuro-viridia glabra nervis subtomentosis exceptis, subtus subtenuiter tomentosa cinereo-viridia, dupliciter crenato-serrata, dentibus ad apicem folii subcurvatis, acutis, apicali quam vicinis multo (c. 3 mm.) longiore, eis nervos primarios terminantibus etiam quam vicinis longioribus; nervi utrinque (9-) 11 (-13), supra vix impressi. *Petala* 6-7 mm. longa. *Fructus* 15-20 mm. longus (siccus), longior quam latus, scarlatinus, lenticellis dispersis mediocribus praecipue basin versus et parvis praeditus.

Holotypus in Herb. Mus. Brit. : v.c. 42, Brecon, lower rocks above Coed Pen-twyn, Mynydd Llangattwg, A. J. Wilmott (no. 4495), 19 September 1933.

A local species replacing *S. aria* in Brecon where it also occurs at Pennwylt (E. F. Warburg, 19 September 1935). It probably also occurs in Montgomery but I have not seen fruiting specimens from there. It is, unlike *S. aria*, not a variable species. The most constant difference from all forms of *S. aria* is in the prominent leaf-teeth. It is tetraploid ($2n = 68$) whereas *S. aria* is diploid.

Sorbus eminens E. F. Warb. [1952, in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 550, fig. 44A (sine diagn. lat.)], sp. nov. *S. ariae* (L.) Crantz et *S. porrigentiformi* mihi affinis, ab illa colore foliorum et fructuum, forma dentium foliorum, ab hac forma foliorum et fructuum inter alia discedit.

Arbor parva vel *arbuscula*. *Folio* ramulorum fertilium ovato-orbiculata vel obovato-orbiculata, (5.5-) 7-10 (-12) cm. longa, 1.1-1.2 (-1.3)-plo longiora quam lata, apice obtusa ad subacuta, basi late cuneata, marginibus basin versus saepe incurvata, parte superiore folii plus minusve rotundata vel latissime triangulari, supra laete viridia sub fructu glabrescentia, subtus tomentosa albido-viridia, margine dupliciter serrata, dentibus praecipuis satis valdosis acutis vel subacuminatis symmetricis quam dentibus ceteris aliquanto longioribus; nervi utrinque (9-) 10-11 (-12); petiolus 1-2 cm. longus. *Folia* ramulorum sterilium brevium saepe minora et angustiora, obovata. *Petala* c. 5 mm. longa. *Antherae* roseo-tinctae. *Fructus* coccineus, satis magnus, usque ad 2 cm. longus, paulo longior quam latus, lenticellis magnis et parvis dispersis praecipue basin versus praeditus.

Holotypus in Herb. Mus. Brit. : v.c. 34, W. Glos., 'Offa's Dyke,' Tidenham, E. F. Warburg (no. 150), September 1935.

This species occurs on Carboniferous Limestone in the Avon Gorge and the Wye Valley and I have seen specimens from v.c. 6, 34, 35, 36. The above description fits plants from the Avon Gorge and from the lower part of the Wye Valley. Round Symond's Yat the shape of the leaves is rather different, the leaves being subrhombic in outline, mostly 1.3-1.4 times as long as broad, and with rather deeper teeth.

Sorbus hibernica E. F. Warb. [1952, in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 551, fig. 44B (sine diagn. lat.)], sp. nov. A *S. porrigentiformi* mihi foliis basi breviter (non longe) cuneatis apice rotundatis, supra haud lucidis differt.

Arbor parva gracilis. *Folia* ovalia vel obovata, (7-) 8-10 (-11) cm. longa, (1.1-) 1.2-1.5 (-1.8)-plo longiora quam lata, apice rotundata, basi late cuneata vel rarius rotundata, marginibus per partem quintam basalem folii rectis integris deinde curvatis serratis, in parte superiore dupliciter serratis haud lobatis, dentibus triangularibus acutis symmetricis, praecipuis quam ceteris longioribus et majoribus, supra sub fructu glabrescentia vel raro basin versus sparse lanata haud lucida, subtus cinereo-viridia subtenuiter tomentosa; nervi utrinque (8-) 9-11 (-12); petiolus 1.2 cm. longus. *Petala* c. 4-5 mm. longa. *Antherae* roseo-tinctae. *Fructus* c. 15 mm. longus, parum latior quam longus, roseo-scarlatinus, lenticellis mediocribus subpaucis praecipue basin versus et parvis paucis praeditus, apice basive paulo lanatus.

Holotypus in Herb. Mus. Brit. : v.c. H 16, W. Galway, Ballynahinch near Recess, E. F. Warburg (no. 247), 26 September 1938.

This species appears to be confined to Ireland where it is widespread across the Centre. It has of recent years been usually referred to *S. porrigens* Hedl. *S. porrigentiformis* does not, however, appear to occur in Ireland.

Sorbus porrigentiformis E. F. Warb. [1952, in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 551, fig. 44c (sine diagn. lat.)], sp. nov. A *S. porrigenti* Hedl. differt foliis longioribus subtus minus tomentosis, fructu subgloboso vel parum latiore quam longo, lenticellis majoribus magis numerosis praedito.

Arbuscula, rarius arbor parva. *Folia* obovata, (5-) 6-9.5 cm. longa, parte superiore plus minusve rotundata, apice obtusa vel breviter acuminata, parte inferiore cuneata marginibus rectis per partem (quartam-) tertiam folii integris, deinde serratis, dentibus triangularibus acutis vel acuminatis symmetricis, praecipuis quam ceteris multo longioribus, matura supra laete viridia glabrescentia satis lucida, subtus albido-viridia subtenuiter tomentosa; nervi utrinque (7-) 8-10 (-11) supra vix impressi; petiolus 8-20 mm. longus. *Petala* c. 5-6 mm. longa. *Antherae* roseae vel roseo-tinctae. *Fructus* subglobosus vel latior quam longus, coccineus, lenticellis subpaucis magnis basin versus praeditus.

Holotypus in Herb. Mus. Brit. : v.c. 34, W. Glos., 'Offa's Dyke,' Tidenham, A. J. Wilmott (no. 4484), 18 September 1933.

This species has usually been called *S. porrigens* Hedl. in this country and was, indeed, originally included in that species by Hedlund. Wilmott (1939, *J. Bot.*, **77**, 206) has, however, chosen the lectotype of *S. porrigens* as Sintenis, 1892 (no. 5128), from Paphlagonia (besides the isotype in Herb. Mus. Brit. which he cites, there is another and better specimen of the same gathering in Herb. Oxford). In view of the existence of certain differences between the British and Asia Minor plants and their wide geographical separation it seems best to regard the British plant as a distinct species.

Plants from different localities in Britain show certain differences and further subdivision may be necessary later. The Wye Valley plants on which the species is typified have, for example, rather narrower leaves than those from other localities. *S. porrigentiformis* occurs in the following v.c.'s : 3, 6, 34, 35, 36, 41, 42, 43, 44, 49.

Sorbus lancastriensis E. F. Warb. [1952, in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 552, fig. 44d (sine diagn. lat.)], sp. nov. Inter *S. rupicolam* (Syme) Hedl. et *S. porrigentiformem* mihi media; ab illa dentibus foliorum symmetricis nervis magis numerosis, lenticellis fructuum minus numerosis nonnullis majoribus; ab hac foliis subtus tomentosioribus, dentibus crassioribus, lenticellis fructuum magis numerosis nonnullis minoribus differt.

Arbuscula. *Folia* (6.5-) 8-11 (-12.5) cm. longa, obovata, (1.4-) 1.5-1.8 (-2.0)-plo longiora quam lata, parte superiore rotundata apice obtusa, basi cuneata marginibus per partem tertiam inferiorem folii saepeissime rectis (in foliis nonnullis magis rotundatis)

integris vel subintegris, deinde serratis, dentibus triangularibus symmetricis acutis vel subacuminatis satis crassis, praecipuis vix prominentibus, matura supra glabra obscure viridia, subtus satis dense cinereo-albido-tomentosa; nervi utrinque (7-) 8-10; petiolus 10-20 mm. longus. Flores, ut videtur, satis parvi. Fructus subglobosus vel latior quam longus, coccineus, lenticellis magnis modice numerosis basin versus et parvis dispersis praeditus.

Holotypus in Herb. Mus. Brit.: v.c. 69, Westmorland, Humphrey Head, E. F. Warburg (no. 234), September 1937.

This species is apparently restricted to several places on Carboniferous Limestone round Morecambe Bay in Lancashire and Westmorland.

Sorbus vexans E. F. Warb. [1952, in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 553, fig. 44F (sine diagn. lat.)], sp. nov. A *S. rupicola* (Syme) Hedl., quae forma foliorum similis est, foliis supra magis lutescentibus, fructu longiore quam lato lenticellis minus numerosis praecipue basin versus positus praedito differt.

Folia obovato-cuneata, (7-) 8-10 (-11) cm. longa, (1.4-) 1.5-1.9 (-2.0)-plo longiora quam lata, apice rotundata, basi cuneata, marginibus per quartam vel tertiam partem inferiorem integris, deinde dupliciter satis crasse crenato-serratis, dentibus satis latis acutis saepissime apicem versus curvatis, nervos primarios terminantibus non majoribus quam aliis, sub fructu supra glabra vel sparse basin versus lanata, subtus albida satis dense tomentosa, subtenuia; nervi utrinque 8-9 (-10); petiolus 1-2 cm. longus. Petala c. 6 mm. longa. Antherae albae. Fructus c. 2 cm. longus, longior quam latus, scarlatinus, apice basique laxe lanatus, lenticellis mediocribus paucis basin versus et parvis paucis dispersis praeditus.

Holotypus in Herb. Mus. Brit.: v.c. 4, N. Devon, wood between Lynmouth and Watersmeet, E. F. Warburg (no. 122), September 1935.

This species appears to be restricted to an area near the coast extending from Lynmouth, N. Devon, to Culbone, S. Somerset. It is noteworthy that, unlike related species, it does not grow on limestone.

Sorbus devoniensis E. F. Warb. [1952, in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 555, fig. 44G (sine diagn. lat.)], sp. nov. A *S. latifolia* (Lam.) Pers et *S. subcuneata* Wilmott foliis basi rotundatis haud cuneatis inter alia differt.

Arbor magna. Folia ovata vel oblongo-ovata rarissime obovata, 7-11 (-12) cm. longa, 1.3-1.6 (-1.8)-plo longiora quam lata, apice acuta vel subacuminata, haud profunde lobata lobis summum octavam partem latitudinis folii attingentibus sed saepissime multo minoribus, late triangularibus acutis acuminatisve, vel vix lobata sed dupliciter serrata, dentibus nervos primarios terminantibus maxime prominentibus rectis, aliis multo minoribus, matura supra obscure viridia glabra, subtus satis inaequaliter viridi-cinereo-tomentosa; nervi utrinque 7-9; petiolus 1-3 cm. longus. Petala c. 7 mm. longa. Antherae albae. Fructus 10-15 mm. longus, subglobosus, brunneo-aurantiacus demum brunneus, lenticellis numerosis basin versus maximis apicem versus magnitudine decrescentibus praeditus.

Holotypus in Herb. Mus. Brit.: v.c. 3, S. Devon, Hoo Meavy, E. F. Warburg (no. 115), September 1934.

This species is widespread over much of Devon, just extending into E. Cornwall. It also occurs, apparently native, in Ireland, in Kilkenny, Wexford and Carlow.

THELYCRANIA (Dumort.) Fourr., 1868, *Ann. Soc. Linn. Lyon*, nouv. sér., **16**, 394. *Cornus* sect. *Thelycrania* Dumort., 1827, *Florul. Belg.*, 83. *Sujda* Opiz, 1852, *Seznam*, 94 (nom. nud.). *Svida* Opiz ex Small, 1903, *Fl. Southeast. U.S.*, 853.

Although the genus *Cornus* L. is still interpreted in a wide sense by the more conservative authors, e.g. Rickett (1942, *Torreyia*, **42**, 14) and Rehder (1949, *Bibl. Cult. Trees & Shrubs*, 495), the modern tendency has been to divide it into a number of smaller genera separated chiefly by characters of the inflorescence, and classifications on these lines have been put forward by Hutchinson (1942, *Ann. Bot.*, new ser., **6**, 83-93) and Pojarkova (1950, *Notul. Syst. Herb. Inst. Bot. Komarov.*, **12**, 164-180). The name *Cornus* was restricted by Hutchinson to the genus containing *C. sanguinea* L. and its allies, which is characterised by the absence of involucre bracts. In thus applying the name *Cornus* Hutchinson was influenced simply by the fact that this particular genus contains more species than the others which are all small: he deliberately rejected as arbitrary the earlier designations of *C. mas* L. as type of *Cornus*. *C. mas*, however, is not an arbitrarily selected type; it is in fact the historic type of *Cornus* and is the species indicated by Linnaeus's validating description of the genus (1754, *Gen. Pl.*, ed. 5, 54) which begins with the phrase "Cal. Involucrum commune tetraphyllum, multiflorum, pedunculiferum: foliolis ovatis, oppositis minoribus, coloratis, deciduis" and thus definitely excludes *C. sanguinea* from consideration as type. The name *Svida* was not validly published until 1903, so that the correct name for the genus containing *C. sanguinea* is *Thelycrania*, based on Dumortier's section of the same name and adopted by Pojarkova.

T. sanguinea (L.) Fourr., Dogwood, is native in the British Isles. Two alien species are found as introductions: *T. alba* (L.) Pojark. and the following.

Thelycrania sericea (L.) Dandy, comb. nov. *Cornus sericea* L., 1771, *Mant. Pl. Alt.*, 199, excl. syn.; Fosberg, 1942, *Bull. Torr. Bot. Club*, **69**, 586. *C. stolonifera* Michx., 1803, *Fl. Bor.-amer.*, **1**, 92; Rickett, 1944, *Brittonia*, **5**, 159; E. F. Warb., 1952, in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 626. *Svida stolonifera* (Michx.) Rydb., 1904, *Bull. Torr. Bot. Club*, **31**, 572. *Thelycrania stolonifera* (Michx.) Pojark., 1950, *Notul. Syst. Herb. Inst. Bot. Komarov.*, **12**, 165.

There has been controversy about the nomenclature of this species under *Cornus*. It is accepted that the type of Linnaeus's *C. sericea* belongs here, but whereas this name is adopted by Fosberg it is rejected as *nomen ambiguum* by Rickett because it has been used for another species. When, however, the species is transferred to *Thelycrania* there is no ground for controversy: the new combination *T. sericea* is applied in the sense of *C. stolonifera* and no ambiguity exists.

J. E. DANDY

Galium tricornutum Dandy, sp. nov. Annu, caulibus tetragonis ut foliorum marginibus retrorse aculeolatis, foliis 6-8-natis lineari-oblongatis mucronatis uninerviis, cymis axillaribus 3-floris, fructu granulato pedicello valde recurvo. *G. tricorne* Stokes, 1787, in With., *Bot. Arrang. Brit. Pl.*, ed. 2, **1**, 153 (nom. illegit.), pro parte, excl. syn. *Valantia aparine*; Sm., 1800, *Fl. Brit.*, **1**, 176; Sm., 1806, *Engl. Bot.*, **23**, t. 1641; et auct. mult. incl. Clapham, 1952, in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 996, fig. 51A.

Holotypus in Herb. Mus. Brit.: v.c. 10, Isle of Wight, "Gathered in June 1806, by Mr. D. Turner and Mr. W. Borrer, in fields near Carisbrook" (Sm., 1806, loc. cit.).

Although this species is widely distributed in Europe, North Africa and temperate Asia, and is well known under the name *G. tricorne*, it is technically *species nova* as it has not in fact been described as a new species. Stokes's original account of *G. tricorne*, and his preceding remarks under *G. spurium*, make it clear that he did not

intend to publish a new species but was identifying our British plant with the known species *Valantia aparine* of Linnaeus. Not only did Stokes cite *V. aparine* L. as a synonym of *G. tricornis* but he quoted (in English translation) Linnaeus's original definition of *V. aparine*. In transferring *V. aparine* to *Galium* Stokes naturally changed the specific epithet in order to avoid homonymy with *G. aparine* L.; but, as *V. aparine* had already been renamed *G. valantia* by Weber (1780) and *G. saccharatum* by Allioni (1785), the name *G. tricornis* is a superfluous substitute and is therefore illegitimate as well as inapplicable to the British species for which it has so long been in use. Smith (1800, loc. cit.) recognised that Stokes had confused two different species, but incorrectly retained the name *G. tricornis* for the British plant while excluding the basynym *Valantia aparine* L. For the species which has been wrongly known as *G. tricornis*, I propose the name *G. tricornutum* so as to restrict the change to a minimum. As holotype I designate the specimen from Sowerby's herbarium (in the British Museum Herbarium) from which plate 1641 of *English Botany* was taken: according to Smith it was gathered in the Isle of Wight by Dawson Turner and William Borrer.

Valantia aparine L., the species with which Stokes identified *G. tricornutum*, is now known as *G. valantia* Weber. As it occurs in Britain occasionally as a casual its synonymy may usefully be given, as follows.

GALIUM VALANTIA Weber, 1780, in Wigg., *Primit. Fl. Holsat.*, 12; Druce, 1920, *Bot. Soc. & Exch. Club Brit. Is.*, 5, 766. *Valantia aparine* L., 1753, *Sp. Pl.*, 1051; non *Galium aparine* L., 1753. *V. triflora* Lam., 1778, *Fl. Franç.*, 3, 384 (nom. illegit.). *Galium saccharatum* All., 1785, *Fl. Pedemont.*, 1, 9 (nom. illegit.); Clapham, 1952, in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 997. *G. tricornis* Stokes, 1787, in With., *Bot. Arrang. Brit. Pl.*, ed. 2, 1, 153 (nom. illegit.), quoad syn. *Valantia aparine*. *G. verrucosum* Sm., 1806, *Fl. Graec. Prodr.*, 1, 93 (nom. illegit.); Sm., 1810, *Engl. Bot.*, 30, t. 2173.

J. E. DANDY

Dactylorchis maculata subsp. *rhومensis* (H.-Harrison f.) H.-Harrison f., comb. nov. *Orchis fuchsii* subsp. *rhومensis* H.-Harrison f., 1949, *Trans. Bot. Soc. Edinb.*, 35, 53; Clapham in Clapham, Tutin & Warb., *Fl. Brit. Isles*, 1318.

J. HESLOP-HARRISON.

REVIEWS

- (a) *Chromosome Botany*. C. D. Darlington. Pp. viii + 186, 36 text figures. Allen and Unwin, Ltd., London, 1956. 16s.
- (b) *Chromosome Atlas of Flowering Plants*. C. D. Darlington and A. P. Wylie. Pp. xix + 519. Allen and Unwin, Ltd., London, 1955; 60s.

The two books under review are the successors of the *Chromosome Atlas of Cultivated Plants*, by Prof. Darlington and Dr. Janaki Ammal, which appeared in 1945. In its new form, the work consists of a Chromosome Atlas, which is in effect a list of chromosome numbers, now extended to cover all the Gymnosperms and Angiosperms which have been investigated, and a short book on Chromosome Botany, which is a development of the introductory essay of the earlier work. The new books are much superior in format and appearance to the old, though the separation of the essay from the list is not entirely an advantage.

The arrangement of the atlas is based on that of Hutchinson with some minor modifications. 241 out of 332 families are represented, and over 15,000 species in 2,500 genera are included. To save space, many of the larger genera, with the greatest constancy of numbers, such as *Quercus* and *Aquilegia*, have been abbreviated, but the necessary references are given. The larger families and genera are appropriately divided into tribes or sections. Each entry has its scientific name, popular name, chromosome number, and reference, the use of the plant is indicated, and its geographical distribution is summarised. There is a full bibliography and a good index.

It is clear that the work of compiling the *Atlas* has been done carefully and critically. Its value to the taxonomist and horticulturalist is obvious, but it is of no less value to the student of evolution. It is unfortunate that it should be so expensive, as this will limit its usefulness. For a work of this type, which is bound to become out of date in a relatively few years, there is much to be said for a low-priced edition even if this means paper and binding of inferior quality.

In the second book under review, the book on Chromosome Botany, Prof. Darlington, in effect, views the material of the *Atlas* in the light of genetic principles and draws conclusions about evolution. He points out that the flowering plants are better understood than any other large group of plants or animals with regard to their ecology and geographical distribution, their breeding behaviour and genetics and the evolution of their chromosomes. In particular, the crop plants, which man has developed and which have in recent years been so extensively studied by genetical methods, provide unique material for the student of evolution.

The first chapter deals with the chromosomes themselves, and the variation in their form and behaviour which can be observed. The second is concerned with the bearing of chromosome studies on the problem of systematic groups, and emphasises the dynamic view of the species to which this leads. The third chapter gives examples of the valuable results that can come from combined cytological and ecogeographical investigation of groups of related plants, as for example in *Rhododendron* and *Oenothera*; and the fourth chapter shows how knowledge of the chromosomes can throw light on the way in which evolution has occurred, on phylogeny, and on rates and modes of evolution. The two concluding chapters, on cultivated and ornamental plants, are of perhaps the most general interest, not only from the evolutionary point of view, but also because these plants are part of our historical and cultural background and tell us a good deal about how and where human civilisation has developed. The brief biographies of the garden flowers, such as hyacinth and daffodil, are well done.

In attempting to summarise, in all its bearings, the subject of Chromosome Botany, the author has undoubtedly succeeded remarkably well. But many of his arguments would be more convincing if they were less condensed. To anyone not so familiar as the author with the original literature, the line of thought is often difficult to follow; and the text has always to be read critically, as there has generally been no space for detailed discussion of individual problems or alternative interpretations. The practice of omitting specific references from the text, though allowing a smoother flow in reading, makes it more difficult to pin down specific points. The result is a book which will be difficult for the amateur who does not already know a good deal about the subject. For the more experienced reader, the book should be most stimulating. It illuminates in an original way the whole story of the evolution of the flowering plants, and it abounds with suggestions and clues which point the way to further investigation and exploration.

D. H. VALENTINE

Bau und Leben der Blumen. Emil Werth. Pp. 204, 46 figures. Ferdinand Enke Verlag, Stuttgart, 1956; DM. 20 (cloth-bound), DM. 18 (stitched).

Professor Werth in this book attempts a solution of that old but still formidable problem, with which such notable names as Delpino, H. Müller and P. Knuth are associated, of how the protean and almost endless variety of flower-forms can be classified on a biological basis. Professor Werth claims to have found the basic principles that enable this to be done, and describes and illustrates sixteen classes in accordance with his views.

Even to summarise his system would here demand too much space; the book itself is a succinct distillation of a dauntingly large body of facts and observations. He considers that the primary, primitive flowers are Napfblumen, "basin-flowers," open, with freely exposed nectar, such as are commonly found in the Ranales. From these, various specialised forms have arisen, involving either contraction of the area occupied by the stamens and styles, often also involving a companulate or tubular shape of the flower; or else elongation and prominence of the stamens and styles in relation to the perianth; or else zygomorphy in various ways. These forms lead on to further specialisation involving temporary trapping of the pollinating visitor, and to reductions through aggregation of the individual flowers and diminution in size, and through loss of nectar to wind and water pollination.

There is a detailed discussion of bird-pollination, with a list (surely very incomplete) of genera and species so pollinated, showing the remarkable preponderance of red or vivid orange in their flowers; and an inevitably speculative account of the evolution of the various flower-forms described by Professor Werth.

This is a stimulating book, based on long experience and much personal observation both in the tropics and temperate regions. It is probable that intermediate forms exist connecting most of his classes, but that they are not thereby necessarily invalidated. It is certain that this book will help to clarify our ideas of flower-forms.

If this book is reprinted the scientific names should be re-checked and the too numerous misprints corrected.

J. P. M. BRENNAN

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OXALIS IN THE BRITISH ISLES

By D. P. YOUNG

INTRODUCTION

The genus *Oxalis* contains nearly 800 species. They occur all over the world, but are mainly subtropical; the two chief strongholds of the genus are South America and South Africa. The only species native in these islands is the well-known wood-sorrel, *O. acetosella*. Many *Oxalis* species, however, have great colonising ability, and have spread far outside their native area, and quite a number have become more or less established in the British Isles. The majority of these introductions have been deliberate, by horticulturalists, and in many cases the spread of a species can be traced back to its origin in a garden.

My efforts to identify various alien *Oxalis* found in this country brought to light serious discrepancies in the naming of previously recorded specimens, which has led me to attempt a revision of the British list. At the same time, the recent spread of some species has been causing concern in horticultural circles, and a general account of the situation may be of interest to botanists.

OXALIS AS WEEDS AND NATURALISED PLANTS

Probably all the naturalised species in Britain have been introduced horticulturally (*O. stricta* may be an exception), and in general they are all plants of open habitats in light or acid soils. As a result, they are very largely confined to growing in garden beds, nurseries and market-gardens, and on walls, gravel paths, rubbish-heaps or seashores near such places. Only rarely do they occur amongst arable crops. *O. articulata* can grow amongst loose grass or brambles, and *O. corniculata*—especially the small creeping forms—is sometimes found in short turf, but none of the other species can (in this country) tolerate the competition of a closed plant community and so their spread is limited by the availability of disturbed ground for them to colonise. Most of the introduced species are native of warmer climates, and so they are not surprisingly commonest and most aggressive in the south-west of England and the Channel and Scilly Isles. Elsewhere they are more frequent near the coast. They also run riot in glasshouses.

The naturalised *Oxalis* fall into two groups, those that reproduce mainly by seed and those that do so mainly by bulbils. The first category includes principally *O. corniculata* and its allies. Although perennial, these can behave as annuals, ripening seed when the plants are only a few months old, and so producing at least one generation a year. Plants of this group are not serious weeds, although they may have a considerable nuisance-value. *O. corniculata* itself has a tough tap-root, which is sometimes difficult to dislodge, and fragile creeping stems which if broken will form separate new plants, but it can be eradicated by frequent cultivation. Forms of this species are common in greenhouses, and are often acquired with potted plants from nurserymen and so are spread to new localities.

It is the species that spread by bulbils that include those that have become a really serious menace. Three species are principally involved. *O. latifolia* is an increasing pest in nurseries and market-gardens in Devon and Cornwall, an established weed in potato fields in Jersey and also in a few nurseries and gardens elsewhere. *O. corymbosa* is a persistent weed in gardens in many parts of the country, especially in greenhouses; it is frequent around London. *O. pes-caprae* is a common weed in the bulbfields in the Scillies.

These three are all sufficiently large and rapid-growing to smother young plants around which they are spreading, and significantly exhaust the nutriment in the soil. Their bulbils are almost indestructible, and are produced in greater numbers if the plants are disturbed or decapitated. The bulbils are formed underground, where they are readily detached and spread around by digging. They are so small that it is quite impossible to comb them out of the soil. The result is that these plants have the property of growing and spreading the faster, the more that attempts are made to dig them out. Bulbils are spread from place to place in soil adhering to digging implements, boots, and transplanted roots, and probably are carried by birds. Peat used for top-dressing has often been blamed as a vehicle, and I have investigated two cases where it was definitely incriminated. Evidently the bulbils get into the peat when in store in nurserymen's yards, either off implements or by the agency of birds.

The problem is not only, or even principally, confined to Britain. *O. pes-caprae* has been an increasing pest in North Africa, and around the Mediterranean generally, since the beginning of the century; it is also a pest in Australia, where it covers great tracts of country. In both these places, in addition to monopolising the soil, it presents the additional nuisance of being poisonous to sheep and cattle. *O. latifolia* is now a well-known weed in many Mediterranean and subtropical countries, and *O. corymbosa* is one of the more serious weeds in Ceylon.

In this country the bulbous *Oxalis* have been established for upwards of forty years and have been troublesome weeds for a good part of that time, but only since the last war has infestation reached alarming proportions. It is difficult to gauge to what extent the increase is real, for many nurserymen in west Cornwall, for instance, claim to have had *O. latifolia* in their ground for years. Nevertheless there is no doubt that in some places this species is rapidly invading new ground, and is increasing in numbers where it is already established. The factor generally blamed is the advent of rotary cultivators, which distribute the soil—and the bulbils—far more effectively than hand digging or even ordinary ploughing. Many of the affected nurseries are in big old gardens which have been converted to the purpose, and *O. latifolia* and *O. corymbosa* seem to have been cultivated in them in their heyday and to have persisted ever since. Possibly another factor has been the revival of flower-growing after the war, which must have involved a great deal of restocking, affording opportunities for the carrying of bulbils to new sites. Furthermore, the plant faces relatively little competition in open cultivated ground, and so its increase is likely to be approximately logarithmic.

The failure of the bulbous *Oxalis* to respond to weed-killers has added to the concern that they are causing. Chemical applications have only the same effect as physical damage, that is stimulating the growth of bulbils which recommence growth as soon as favourable conditions return. Ducellier (1923) recognised that the only chance of killing the plants was to use a powerful herbicide (he recommended 10—20% sulphuric acid) at frequent intervals during the short time between the shrivelling of the old bulb and formation of new bulbils. Modern workers have aimed at killing the bulbils themselves, and fumigation with agents such as methyl bromide (originally developed against animal pests in the soil) has shown the most promise so far (Luckwill 1953, 626—627). Fumigation is very expensive and would be quite uneconomic for an individual grower to carry out except under glass where the ground is valuable. It seems, therefore, that even if control of *Oxalis* infestation by this means is successful, its application would require mutual or government financing. To what extent infestation must progress before it becomes in the public interest to do this remains to be seen. Some hopes have been expressed that a natural predator might be found, suitable for biological control. No active work seems to be being done on this rather tenuous line of attack. The nearest approach to such a

method has been the partly successful use of pigs or poultry to rout for the bulbils. It is possible to choke out the plants by grassing over the land for three years or more—until all dormant bulbs have died. But the owner of the ground usually depends for his livelihood on the regular cropping of the land with flowers or vegetables, and so here again the remedy is economically out of the question for an individual. Moreover, it is important to clear the whole of an infested tract, as otherwise a cleared patch will soon be reinfested from neighbouring *Oxalis* colonies.

It is often difficult to decide whether *Oxalis* in gardens are to be considered wild or not. The fact that a plant can maintain itself in a garden where it was planted, without further care from the gardener, is not sufficient to justify calling it feral. The real criterion is whether it can withstand efforts to exterminate it. As far as most bulbous species are concerned, the facts just given speak for themselves. In the case of the less unwelcome species, one cannot be so definite. The records given below are all considered to be feral, but some have been given the benefit of the doubt. Details of habitat have been included as far as possible to allow the reader to form his own conclusions. "In gardens" is intended to imply that the plants were at least not part of the cultivation scheme. Herbarium specimens have been accepted as feral unless the labels indicated that they were cultivated.

TAXONOMY

The genus is one of considerable difficulty, in the first instance because it includes many groups of closely related forms, which are variously regarded according to the state of knowledge of them as single polymorphic species or as groups of critically-defined species. The original range of variation of several species has unfortunately been obscured by the fact that selected strains have been collected and bred by horticulturalists, and have since returned to the feral state. Many of these reproduce only vegetatively, and apparently distinct and constant forms are only clones. This complexity has led to considerable difficulties with nomenclature, which will be appreciated by studying the account of the few species below. There are undoubtedly many more names than species, but progress in clearing up synonymy has been hampered by lack of knowledge of natural ranges of variation on one hand, and by inadequate descriptions and type-specimens on the other.

The genus has been monographed by Knuth (1930), but his account has been criticised on the grounds of excessive subdivision and separation of closely related taxa, and of the inclusion of the same species under two or more different names. As a source-book it is nevertheless invaluable. A treatment of the South African species on more satisfactory lines is given by Salter (1944), who studied the plants in the field for many years. Wiegand (1925) revised the *Corniculatae* group from the eastern United States, and his version has been adopted by Fernald (1950, 943-946) in the latest edition of Gray's *Manual of Botany*. A new investigation of the genus in South America, based on field observations, is badly needed. For the present, any piecemeal alterations in nomenclature are inadvisable unless based on very solid evidence.

The following account of the naturalised British species adopts the arrangement of Knuth's monograph, except that the section *Polyoxalis* (*O. tetraphylla*) is merged with *Ionoxalis*. The treatment of the *Corniculatae* is based mainly on Wiegand's revision. No attempt has been made to cite complete synonymies, for which reference should be made (with caution!) to the works already mentioned. The names adopted are those that seem most generally acceptable; although many of them are open to objection, a lengthy taxonomic investigation will be needed before the nomenclature can be properly settled. Species reported as British, but on inadequate evidence, are included in square brackets.

DESCRIPTION OF THE BRITISH SPECIES

All our species except *O. tetraphylla* have trifoliolate leaves, and this is to be understood in the descriptions. Most of them flower all through the summer, and flowering times are only mentioned where they are more restricted.

The abbreviations used for herbaria are those of the *Index Herbariorum*, viz. : BM British Museum, CGE Cambridge University, K Kew, MANCH Manchester Museum, NMW Cardiff Museum, OXF Oxford University, SLBI South London Botanical Institute. Records with no date are recent, i.e. since 1950 and believed to be still extant; undated herbarium specimens are denoted by "n.d." Records marked ! have been seen by myself in situ. "Teste" before a collector's name implies that I have accepted the record without seeing a specimen.

Section LAXAE Reiche. No bulb. Stem short, erect, herbaceous. Inflorescence cymose. Flowers yellow.

O. VALDIVIENSIS Barnéoud, 1845, in Gay, *Fl. Chilena*, 1, 446.

Annual. Whole plant *glabrous* or almost so. Stem short (10 cm.) or almost absent. Leaves closely scattered up the stem; petioles long (4-14 cm.), sometimes minutely pilose, with a joint about 5 mm. from the base, below which they widen out into tapering sheaths. Peduncles much longer than the leaves (8-15 cm.), bearing flowers in long *forked cymes*. *Sepals obtuse*, 4 mm. *Petals* 12-16 mm. long, yellow with *reddish veins*. *Pedicels* reflexed in fruit, capsules *pointing downwards*. *Capsule short* (6 mm.), nearly spherical, scarcely longer than the calyx.

Native of Chile, on woodland margins. In cultivation, but not very commonly grown. Has occurred rarely in this country as a garden escape or relic of cultivation, often only casual.

- V.c. 5. S. SOMERSET : no locality or date, but apparently from the Ilminster region ca. 1921, *H. Downes* (BM); "Seems to be a casual . . . It was found far in the country, but I think it might have been introduced with corn refuse spread on the land."
 8. S. WILTS. : apparently wild in a garden and adjacent waste land, Larkhill, 1941, *R. C. L. Burges* (hba. Burges, J. D. Grose).
 23. OXFORD : maintains itself in a garden at Burford, teste *D. McClintock*.
 29. CAMBR. : waste ground, Cambridge, 1882, *N. & H. N. Dixon* (SLBI).
 36. HEREF. : casual, Underdown, Ledbury, 1901, *S. H. Bickham* (BM).

Only the Somerset specimen had previously been correctly determined, but the record has not been published heretofore. I have heard of other gardens where it "runs wild," but it is scarcely feral.

[Section ROSEAE Reiche. No bulb. Stem \pm erect, herbaceous. Corolla pink. S. America.

O. ROSEA Jacquin, 1794, 25.

Annual, 20-40 cm. tall. Stem simple or branched, juicy, glabrous, bearing small scattered leaves. Petioles short (3 cm.); leaflets glabrous or slightly pilose, obcordate, up to 10 mm. long. Inflorescence a few-flowered forked cyme; peduncles up to 10 cm. long, pedicels 0.5-1 cm., erect in flower, drooping in bud and in fruit. Petals about 5 mm. long, retuse, rose-pink with a whitish base. Capsule globose.

Native of Chile, in meadows. Long cultivated as a garden and greenhouse plant, but not often seen nowadays. Sometimes considered, quite incorrectly, to be synonymous with *O. floribunda* Lehm. (i.e. *O. articulata* Savigny), whence much confusion has arisen amongst gardeners and botanists who have used either name for both species. Occasionally maintains itself in gardens, but there are no authentic records for it occurring wild in this country. The record by Druce (1932) is based on a specimen of *O. articulata*.]

Section CORNICULATAE Reiche. No bulb. Stem weakly erect, procumbent, or creeping. Flowers yellow. Cosmopolitan, centred on America.

The plants of this critical section show a complex reticulation of characters, particularly the pubescence of various parts. The position is further complicated by a long-standing dispute over the nomenclature of the three chief species. The following table shows the names adopted by various authors for the three taxa, which may be represented by their *B.P.L.* (ed. 2) numbers.

<i>B.P.L.</i> number	132/2	132/3	132/4
<i>B.P.L.</i> name	<i>corniculata</i> L.	<i>stricta</i> L.	<i>dillenii</i> Jacq.
Salisbury (1794)	<i>pusilla</i>	<i>ambigua</i>	
Jacquin (1794)	{ <i>corniculata</i> L. <i>repens</i> Thunb.	<i>stricta</i> L.	<i>dillenii</i>
Jordan (1854)		<i>europaea</i>	<i>navieri</i>
Small (1896)	<i>corniculata</i> L.	<i>cymosa</i>	<i>stricta</i> L.
Robinson (1906)	<i>repens</i> Thunb.	<i>corniculata</i> L.	<i>stricta</i> L.
Wilmott (1915)	<i>corniculata</i> L.	<i>stricta</i> L.	
Wiegand (1925)	<i>corniculata</i> L.	<i>europaea</i> Jord.	<i>stricta</i> L.
Eiten (1955)	<i>corniculata</i> L.	<i>stricta</i> L.	<i>dillenii</i> Jacq.

The views of Wiegand are adopted here as far as species are concerned. His treatment is a hierarchy of species, varieties, and forms; many of his infra-specific taxa are artificial, but may be useful for classification.

A list of distributed exsiccata from this group, with corrected determinations, is given in Appendix II.

O. CORNICULATA L., 1753, *Sp. Pl.*, 435.

Stems radiating from a fusiform tap-root, prostrate or procumbent, 10-30 cm. long; rooting freely at the nodes and occasionally buried, but specialised stolons lacking; usually pubescent. *Leaves alternate*; petioles with *oblong stipules* at the base (fig. 1A), with spreading pubescence; leaflets cuneate-obcordate, glabrous above, sparingly pubescent beneath. *Peduncles* slightly longer than the leaves, *pubescent*, bearing 1-7 flowers in an *umbel*. *Sepals* 2.5-5 mm., *acute*: petals bright yellow, 4-7 mm. *Capsule* angular-cylindrical, *hoary* with reversed adpressed pubescence and with some patent hairs.

Varieties.

This species is exceedingly variable, and the forms breed true from seed.

Var. CORNICULATA represents the typical or normal-sized plant: stems up to 50 cm. long, sometimes ascending; leaflets 8-23 mm. broad; inflorescence 2-7 flowered; capsules 12-25 × 3-4 mm.

(i) *Dwarf forms*.—There appear to be more than one of these, but taxonomy and nomenclature are both unsatisfactory, and I can only offer the following tentative arrangement:

Var. REPENS (Thunb.) Zuccarini, 1829-30, *Denkschr. Akad. Münch.* 1 abh., 230; O. *repens* Thunberg, 1781, *Oxalis*, 16. Stems filiform, prostrate, often creeping underground; leaflets 6-12 mm. broad; inflorescence 1-2 - flowered, rarely more; capsules 12-16 × 3-4 mm. This is probably identical with var. *minor* Lange (1880, in Willkomm

& Lange, *Prod. Fl. Hispan.*, 3, 520) which name is often used but is antedated by var. *minor* Ecklon & Zeyher (1835, *Enum. Plant. Afr. Austr. Extratrop.*, 83), "foliis obcordato-cuneiformibus glauco-puberulis minoribus," which may not be the same thing. Apparently a native of S. Africa; often grown in gardens, especially as a purple-leaved form (see below). Probably not infrequent as a garden escape, but I hesitate to give any records owing to the difficulty of separating it from var. *corniculata* which has been dwarfed by conditions of growth. When grown side by side the two are nevertheless distinct.

Var. **MICROPHYLLA** Hooker f., 1864, *Handbook of the N.Z. Flora*, 38; *O. microphylla* A. Cunningham ex Hooker f. (*loc. cit. in syn.*), non Poirlet, 1816, *Encycl. Méthod., Bot.*, suppl. 4, 248 (= *O. bifida* Thunb.). Plant forming a low compact mat of wiry creeping stems and tiny leaves; petioles 0.6-1.3 cm., filiform; leaflets rather deeply emarginate, 3-6 mm. broad; *peduncles* filiform, *one-flowered*; *capsules* short, 5-7 × 3 mm., abruptly narrowed at the top. Mountainous parts of New Zealand and Tasmania. Often grown in rockeries. A frequent garden escape which becomes established in gravel paths, between paving stones, and sometimes in lawns and other short turf. It can be distinguished with certainty by the short fat capsules, and in habit it is quite distinct. It probably merits the rank of a geographical subspecies. Recorded in Britain as follows:

- V.c. 2. E. CORNWALL : Newquay, 1913, C. C. Vigurs (K).
 6. N. SOMERSET : Bruton, 1937, F. K. Makins (K).
 11. S. HANTS : Beaulieu Abbey, 1926, R. Findlay (K).
 16. W. KENT : on gravel road verge, Tunbridge Wells, K. E. Bull!
 17. SURREY : foot of wall, Holmbury Hill, 1932, E. C. Wallace (hb. J. E. Lousley).
 21. MIDDX. : Ealing, 1949, L. M. P. Small (BM).
 33. E. GLOS. : in a lawn, Cheltenham; on a footpath, Gretton, N. Saunders (hb. Young).
 35. MON. : garden weed, Newport, 1955, K. F. Adams (NMW).
 36. HEREF. : Ledbury, 1917, S. H. Bickham (K).
 38. WARWICK : near river below the castle, Warwick, B. T. Ward.
 44. CARM. : roads and footways, Achddu [? Fachddu], 1944, J. A. Webb (NMW).
 58. CHESHIRE : gravel road verge, Prenton, Birkenhead, E. P. A. Jones! (hb. Young).
 62. N.E. YORK : Thornton-le-Dale, 1915, E. C. Horrell (OXF).
 74. WIGTOWN : garden weeds, Newton Stewart and Logan, R. C. L. Howitt (hb. Young).
 H38. DOWN : Singer's nurseries, Newcastle, teste D. McClintock.
 H39. ANTRIM : garden weed, Rathmore, Greenisland, *idem*.
 S. CHANNEL IS. : old walls, St. Peter Port, Guernsey, 1928, R. M. Hall (BM).

(ii) *Anthocyanin varieties*.—Various forms with the vegetative parts suffused with purple are grown in gardens. The nomenclature is unsatisfactory; the arrangement given by Knuth (1930, 149-150) is incorrect.

Var. **ATROPURPUREA** Van Houtte ex Planchon, 1857, *Fl. des Serres*, 2(2), 47 & t. 1205, "foliis atropurpureis." This is apparently the same as var. *purpurea* Parlatores (1872, *Fl. Italiana*, 5, 271), "caule foliisque purpureis," and var. *rubra* Nicholson (1886, *Ill. Dict. of Gardening*, 2, 540), "dark purple leaflets," and Planchon (*loc. cit.*) cites *O. tropaeoloides* Schlachter (ined.) as synonymous. Identical with var. *corniculata* except that all parts normally green are heavily suffused with purple. The coloration tends to fade on drying, so that pressed specimens turn ± green. A frequent garden escape or relic of cultivation; records not worth listing in full, but a few will be found in Appendix I.

Besides the above, a purple-suffused form of var. *repens* exists. Unless one of the above names is applicable, there seems to be no separate name for it. It is frequent as a garden weed. Var. *variegata* Goiran (1896, *Bull. Soc. Bot. Ital.*, 97), "foliis \pm variegatis," is a form completely suffused with purple but with the leaves flaked with achlorophyllose patches, resulting in a harlequin pattern of brownish-purple and bright rose (see plate in *Fl. des Serres*, 19, t. 1968 (1873)). I have not seen true *variegata* in this country.

Numerous other varieties have been described, notably var. *villosa* Hohenacker with hairy leaves and stems, but none occurs in this country.

Distribution

The aggregate *O. corniculata* is cosmopolitan, but is probably not indigenous over much of its range. It does appear to belong to the Old World. It is chiefly grown in gardens as the varieties mentioned above. Different strains vary in hardiness, but some will stand the hardest winter even if top growth is killed, and all can overwinter as seeds. On the continent it is a frequent weed of disturbed ground, dry roadsides, etc. In this country it is most frequent as a garden weed, and the earliest record of its spontaneous appearance was no less than 370 years ago (Raven 1953, 14). The varieties are usually more or less obvious escapes or relics of cultivation, but are none the less very persistent, and are spread with pot plants and the like from nurseries. The plant is most frequent in the south-west, and is very common in the Channel Isles. It is known from vice-counties 1-3, 5, 6, 8-17, 20-28, 30-36, 38, 40, 41, 43, 44, 46-49, 51, 54-64, 68-70, 72, 74, 77, 83, 85, 86, 88, 91, 93, H21, H38, H39, and the Channel Isles. The list given in the *Comital Flora* is very incomplete, and that just given contains many vice-counties not included in the *C.F.* or subsequent publications. These are technically new county records and are enumerated in Appendix I.

O. STRICTA L., 1753, *Sp. Pl.*, 435, sec. Small (1896). *O. dillenii* Jacquin (1794); *O. navieri* Jordan (1854).

Root fibrous. Stem often branched from the base, strigose, rather fleshy; erect or decumbent, occasionally rooting but *without specialised stolons*. Leaves *subopposite or in groups* or fascicles; *stipules narrow*, oblong, adnate to the petiole (fig. 1B); petioles strigose; leaflets *obcordate*, 10-18 mm. broad, glabrous on both sides or sometimes with a few hairs beneath. Peduncles longer than the leaves, strigose; *inflorescence* (1-)2-3(-4) flowered,

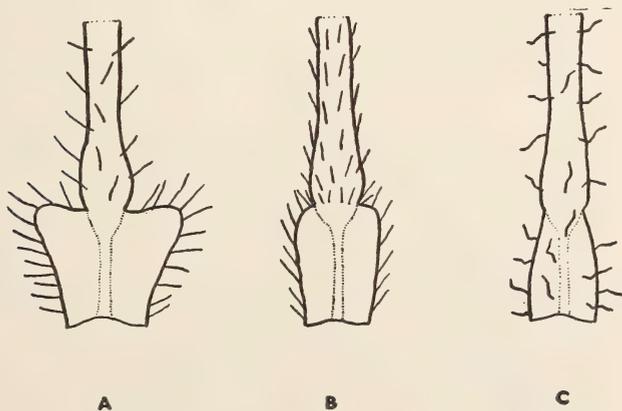


Fig. 1. Leaf-bases of (A) *Oxalis corniculata*, (B) *O. stricta*, (C) *O. europaea*. $\times 8$.

umbellate, not cymose; pedicels 8-25 mm. long, deflexed in fruit, strigose. Petals 7-11 mm. long, soft yellow. Capsules cylindrical, 15-25 × 3 mm., abruptly short-pointed. The plant occurring here appears to come under var. *piletocarpa* Wiegand (1925), which has the capsule finely and densely adpressed-puberulent but not viscid. According to Wiegand, in the type it is finely puberulent with additional long viscid hairs. Flowers from August onward.

Canada and U.S.; rarely cultivated or adventive in Europe. Wiegand says, "When and how widely this species was introduced into Europe is not known . . . It was evidently growing in the Eltham garden at the time of Dillenius, but seems not to have spread as did *O. europaea*." It occurs here and there in France (Chevalier, 1940, 675); I have seen it in the Jardin des Plantes in Paris, mixed with *O. europaea*. Although frost-hardy to some extent, it seldom survives the winter and behaves as an annual.

Only British station, v.c. 13, W. Sussex; in arable fields on sandy soil near Pulborough, 1951, *O. Buckle*; has persisted since. How or whence it was introduced here is not known. It appears in greatest quantity amongst root-crops, or in stubble after the corn is cut; the agrestal habitat is noteworthy. An earlier record from Cemmaes, v.c. 47 (Druce, 1920), on the strength of which the plant already appears in the *B.P.L.*, is incorrect; the specimen (OXF) is *O. europaea*.

O. EUROPAEA Jordan, 1854. *O. stricta* mult. auct. (incl. *B.P.L.* ed. 2, *Fl. British Is.*, and, *Student's Flora*).

Short-lived perennial or annual. Root fibrous. Stem usually erect, 5-40 cm. tall, glabrous or hirsute with septate hairs; emitting underground stolons from the base, and also sometimes horizontal, but not rooting, branches above ground. Leaves mostly subopposite, fascicled, or whorled; stipules none, or no more than a narrow wing to the enlarged basal joint of the petiole (fig. 1C); petioles (and peduncles) glabrous or strigose; leaflets obcordate, 12-30 mm. broad, typically glabrous. Peduncles about as long as petioles; inflorescence of 2-5 flowers, often cymose; pedicels 8-10 mm. long, not reflexed in fruit. Petals 5-10 mm. long, yellow. Capsule cylindrical, shorter than in the last two species (8-12 × 2.5-3.5 mm.), gradually acuminate, glabrous or with only scattered hairs. Flowers from July onward.

Varieties.

(i) *Indumentum variation*.—The plant varies a good deal in the hairiness of various parts, and different combinations of characters are possible. Wiegand (1925, 135) gives an arrangement which may be summarised as follows:

		Upper surface of leaves glabrous	Upper surface of leaves hairy
		var. <i>europaea</i>	var. <i>bushii</i>
Hairs on pedicels adpressed, not viscid	{ Stem glabrous or with adpressed hairs Stem villous	f. <i>europaea</i>	f. <i>subglabrata</i> Wiegand
		f. <i>pilosella</i> Wiegand	f. <i>bushii</i>
Hairs on pedicels spreading, viscid	{ Stem nearly or quite glabrous Stem villous	f. <i>cymosa</i> (Small) Wiegand	—————
		f. <i>villicaulis</i> Wiegand	f. <i>vestita</i> Wiegand

Var. *BUSHII* (Small) Wiegand, 1925, 135; *O. bushii* Small, 1898, 611, with leaves covered with adpressed hairs, is a distinct enough plant. It is quite rare in this country and has not indeed been collected since last century. Records: v.c. 1, W. Cornwall; near Penzance, 1839, *J. Ralfs* (MANCH); 1872, *Mrs. Lomax* (BM, etc.), and many intermediate dates but none subsequently. 41, Glam.; "Glamorgan," 1850, *J. W. Rimmington* (MANCH)—a rather dubious record.

As to the various forms proposed by Wiegand, the variation in stem and pedicel indumentum is so wide and apparently inconstant—depending amongst other things on the state of development of the plant—that I refrain from quoting any British records under the separate names. Nothing appears to be known of the genetics of the various characters, and although his names may be useful for classifying herbarium specimens, their scientific basis is doubtful.

(ii) *Anthocyanin variety*.

Var. *rufa*, (Small) comb. nov. *Oxalis rufa* Small, 1901, in Britton, *Manual Fl. N.W. States and Canada*, 577; *O. stricta* var. *rufa* Farwell, 1918, *Rep. Mich. Acad. Sci.*, **20**, 183. Leaves and to a lesser extent stems etc., suffused with reddish-purple. The colour, which disappears in old leaves and also very largely on drying, is pinker and less intense than in the parallel variety of *O. corniculata*. Occurs not infrequently as a naturalised weed, but I have not seen it outside gardens. Records too numerous to give in detail; some are given in the Appendices.

A prostrate form, var. *lejeunei* (Rouy) Chevalier (1940, 675), has been described. I have seen no material and am inclined to doubt whether it is distinct.

DISTRIBUTION

Despite Jordan's name, *O. europaea* is almost certainly only native in N. America and possibly Japan and Manchuria, but it is naturalised almost ubiquitously. In Britain it is chiefly a garden weed, but it has occasionally been recorded in arable crops including corn. Like *O. corniculata* it tends to behave as an annual. It is common on the light soils of west Surrey, and in the adjoining parts of Middlesex and west Sussex; elsewhere it has occurred in localities scattered rather evenly over the whole country except the north of Scotland. It is not particularly common in the south-west, and is only doubtfully recorded from the Channel Isles. This distribution, which may be contrasted with that of *O. corniculata*, is an expression of the plant's preference for a cool temperature climate. Recorded for v.c. 1-14, 16-18, 21-26, 28, 29, 33, 37, 38, 41, 44, 47-49, 52-59, 68, 70, 74, 80, 83, 87, 93, 94, H22, H38, H39, and Donegal. Here again the C.F. is very incomplete and the above lists contain many technically new county records which are substantiated in Appendix I.

Section *CARNOSAE* Reiche. Perennials with thick stems, tuber-like but not bulbous at the base, bearing leaves at the growing tip. Xerophytes from Chile.

O. CARNOSA Molina, 1810, *Sagg. Storia Nat. Chile*, 2nd ed., 288.

A succulent with fleshy stems, 1-2 cm. in diameter, at first subterranean but becoming aerial by gradual lengthening, eventually attaining 20 cm. long, branched, pitted with the scars of old leaf-bases. Whole plant glabrous. Leaves and flowers borne at the tips of the stems. *Leaflets fleshy*, up to 2 cm. broad, obcordate, smooth and somewhat glaucous above, entirely covered below with glistening transparent papillae which give the surface a crystalline appearance. Peduncles somewhat longer than the leaves, bearing 1-3 (-5) flowers in an umbel. *Three outside sepals cordate-deltoid with prominent auricles*, two

larger than the others and clasping the unopened corolla in bud, the third folded back about its midrib; two inner sepals much smaller, linear. *Petals* ca. 15 mm. long, *bright yellow*. Capsule short, oblong, 7 mm. long, about equalling the sepals; setting good seed in this country.

Native of Chile, mainly on coastal rocks. Grown as a greenhouse plant; very frost-sensitive so will not pass the winter out of doors except in frost-free localities. A member of a critical group, but apparently the only species cultivated. Very difficult to make into satisfactory pressed specimens; if dried in the ordinary way, the plant breaks at every joint and falls to a heap of fragments.

Naturalised on walls and banks on St. Mary's and Tresco, Scilly Isles, probably planted (see discussion in *Proc. Bot. Soc. Brit. Is.*, **1**, 578 (1955)). Known there for some 20 years, but the earliest specimen that I have seen was collected by R.C.L. Burges in 1950 (hb. Burges).

Section ARTICULATAE R. Knuth. Perennials with thick woody rootstock bearing leaves at the growing point.

O. ARTICULATA Savigny, 1798, in Lamarck, *Encycl. Méthod., Bot.*, **4**, 686. *O. lasiopetala* Zuccarini, 1825, 25; *O. floribunda* Lehmann, 1826, *Ind. Sem. Hort. Hamburg*, 17.

Rhizome thick, fleshy or almost woody, ascending or horizontal, up to 2 cm. diameter, covered with the scars or scaly remains of old leaf-bases, and with a wiry basal root; in old plants becoming branched, often with constrictions which divide it into spherical or oblong segments; very like the rhizomes of *Iris germanica* but smaller. Leaves and flowers borne at the ends of the rhizomes, so that the plant forms compact bunches. Petioles 10-25 cm. long, \pm pubescent; *leaflets* obcordate, \pm pubescent, 1-4 cm. broad, with sparse but prominent elongated orange calli all over both sides, although concentrated on the underneath margin (fig. 2a). Peduncles slightly longer than the petioles. Flowers many, in an umbel; sepals with an orange callus at the tip, pubescent; petals 10-15 mm. long, usually bright deep rose colour, rarely white or pale pink. Capsules cylindrical-ovate, short (10 mm.), not plentifully formed.

It is difficult to say what is the correct name for this well-known garden plant. It is commonly known as *O. floribunda*, which is equated by Urban (1884) and Knuth (1930, 210) to *O. articulata* var. *hirsuta* Progel (1877, 488); but I think the latter name should be restricted to heavily tomentose forms. Chevalier (1940, 692) considers that the common plant is *O. lasiopetala* and that it is not the same as *O. floribunda*. Knuth (1930, 196, 208) separates *O. lasiopetala* from *O. articulata* by lack of subfoliar tubercles in the former, evidently relying on Zuccarini's omission to mention them. However, the isotype ("Brasilia. Sellow legit," ex herb. Berlin) of *O. lasiopetala* at Kew has tubercled leaves, so this distinction will not hold water. Chittenden (1951, 1458-1460) considers that the garden *O. floribunda* is partly *O. rubra* St.-Hilaire (1825, *Fl. Bras. Mer.*, **1**, 124), but I know of nothing to support this view. *O. floribunda* has also been equated to *O. martiana* (see below), and confused with *O. rosea* following a misnamed plate in the *Botanical Register* (**13**, t. 1123 (1827)). Pending a reinvestigation of the taxonomic position, it seems best to keep to the oldest name, with the reservation that it may have to be understood in an aggregate sense to cover the group of plants from which the cultivated plant has been derived.

Native of E. temperate South America; occasionally naturalised in other temperate countries. A favourite garden plant, and nowadays by far the commonest pink *Oxalis* in cultivation. It is hardy, but flourishes best in warmer areas.

Found \pm naturalised in waste ground, roadsides, and seashores, always near houses and only becoming well established near the coast (on account of the milder climate); frequent in the south-west. Rarely becomes a weed, and unlike other species is often found amongst other vegetation such as grass or brambles.

- V.c. 1. W. CORNWALL : Gulval, 1952, *M. L. Bolitho* (hb. J. E. Lousley); roadside, Lizard, *B. D. Miles*; frequent in the Scillies!, sometimes a bulbfield weed, teste *R. C. L. Howitt*.
2. E. CORNWALL : waste-ground, Newquay, 1931, *G. C. Druce* (OXF); meadow, Polzeath, 1935, *J. D. Grose* (hb. Grose).
3. S. DEVON : Dartmouth, 1930, *F. M. Day* (OXF).
11. S. HANTS. : Milford, 1935, *I. W. Wyatt* (K).
13. W. SUSSEX : seashore, amongst grass and brambles, Kingston!
16. W. KENT : old gravel-pit, Hayes, 1912, *W. H. Griffin* (OXF, SLBI).
44. CARM. : Llanstephan, 1920, *D. Hamer* (OXF).
45. PEMB. : hedges, Newgale Hill, 1947, *J. A. Webb* (NMW).
48. MERION. : on shingle between Barmouth and Llanaber, 1926, *C. E. Salmon* (K).
55. (RUTLAND) : old stone heaps far from houses, Ketton; also at Ryhall, *R. C. L. Howitt*.
- H1. KERRY : sandhills near houses, Derrynane, 1937, *R. C. L. Burges* (hba. Burges and J. E. Lousley).
- H20. WICKLOW : sandhills, Brittas Bay, 1937, *idem* (*ibid*).
- H21. DUBLIN : amongst brambles, Hill of Howth!
- S. CHANNEL IS. : frequent, *D. McClintock* (BM).

Section OXALIS. Perennials, with a herbaceous horizontal creeping rhizome, often scaly. Leaves trifoliolate; flowers solitary. A widespread group of closely-related species.

O. ACETOSELLA L., 1753, *Sp. Pl.*, 433.

The common wood-sorrel, and too well-known to need description. The flower-colour varies, and forms have been distinguished as vars. *alba* Peterm. (= type, i.e. should be called var. *acetosella*), *rosea* Peterm., *subpurpurascens* DC., *purpurascens* Mart., *lilacina* Lange, *violacea* Westf., and *caerulea* DC.

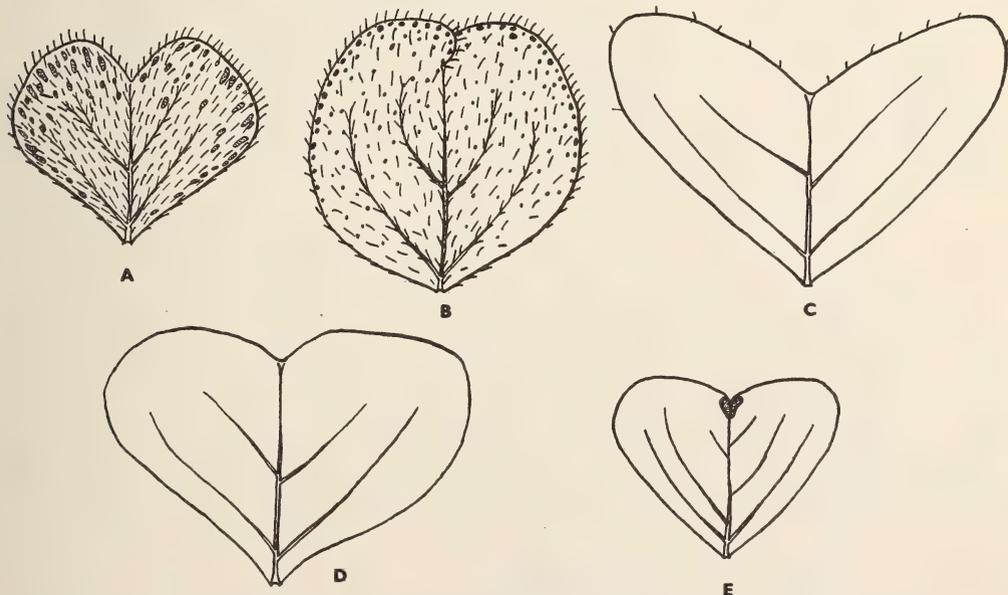


Fig. 2. Underside of single leaflets of (A) *Oxalis articulata*, (B) *O. corymbosa*, (C) *O. latifolia* ("typical" form), (D) *O. latifolia* from Cornwall, (E) *O. violacea*. Natural size.

Throughout Europe and northern Asia. Represented in America by the closely-allied *O. montana* Raf. and *O. oregana* Nutt.

Section IONOXALIS (Small) R. Knuth. Plant stemless; leaves and flowers springing from a bulb formed by the bases of the petioles enlarged into scales. N. and S. America.

Another difficult group; the entire plant including bulb is essential for identification. The species in cultivation, and hence those that have become naturalised outside their native area, propagate themselves to a great extent vegetatively. They thus form clones derived from a few selected forms, and it is impossible to draw any taxonomic conclusions by studying them.

O. CORYMBOSA DC., 1824, *Prod.*, **1**, 696. *O. martiana* Zuccarini, 1825, 20.

Leaves and flowers springing from an underground bulb (fig. 3A) with ovate scales, pale brown outside and whitish inside; when mature the bulb develops into a *large mass of bulbils* (3-6 mm.) all *sessile* in the axils of the old scales, which wither and leave only the heart of the original bulb unchanged. One or two roots from the base of the bulb often swell into juicy white translucent tubers up to 5 cm. long and 1 cm. thick at the top. Petioles weak, thin and tortuous below ground, sparsely hairy, 5-15 cm. long; *leaflets* (fig. 2b) large, 2.5-5.5 cm. wide, roundish, *with a deep narrow indentation* at the apex between rounded, close or even overlapping lobes; sparsely *hairy* beneath and near the margin above, and *with tiny reddish calli* on the margin and microscopic reddish tubercles (hardly visible to the naked eye) scattered over the lower surface. Peduncles up to 30 cm. long, bearing flowers in a *contracted cyme*. Sepals acute, with two orange calli at the tip. Petals purplish rose, 15-20 mm. long. I have never seen the fruit, nor a description of it. The plant spreads by the bulbils which are copiously produced in autumn.

De Candolle's name antedates the better-known *martiana* by a few months. It is threatened by two earlier names, *O. debilis* Kunth (see below) and *O. macrophylla* Kunth, 1821, in Humboldt, Bonpland, and Kunth, *Nov. Gen. et. Spec.*, **5**, 184, but there is some doubt as to whether they are conspecific. The equation of *O. martiana* Zucc. to *O. floribunda* Lehm. in the *B.P.L.* (ed. 2), copying Progel (1877, 486), is quite erroneous.

Superficially resembles *O. articulata*, from which it can be distinguished by the laxer habit, characteristic cluster of bulbils, and different calli underneath the leaves. It is more difficult to separate from the following species, the descriptions of which should be consulted.

Native of most of South America; naturalised in many subtropical countries and a troublesome weed in some. Formerly cultivated as a garden plant, but quite superseded by *O. articulata* which is much more floriferous and much less dangerous.

Rather frequently naturalised in old gardens, where it is usually a relic of cultivation. Unlike *O. articulata* it cannot compete in closed associations and is only seen in open tilled ground, paths, etc. Occasionally in market gardens and nurseries, usually where an old garden has been turned to such use; sometimes distributed with nurseryman's plants and peat. Common in suburban gardens west and south of London, probably emanating from various parks and botanical gardens, some of which have since been built over; occasional in other parts of the country, but in Cornwall and Devon less common than *O. latifolia*.

V.c. 1. W. CORNWALL: nursery, Penzance!

8. S. WILTS.: Cathedral Close, Salisbury, R. C. L. Howitt.

11. S. HANTS.: Southampton University botanic garden! garden, Chandler's Ford!

14. E. SUSSEX: cottage gardens, Mayfield! and Battle!

16. W. KENT : Greenwich Park! (evidently the plant recorded, as *O. floribunda*, by Grinling, Ingram, and Polkinghorne (1909)); in market-garden and glasshouses, Oakley House, Keston, *R. Woodall*!; spreading from the gardens of Fairhill House, Shipbourne, and now over a half-mile radius, *R. Bush*!
17. SURREY : frequent in the London suburbs from Kew to Croydon!; Kew Gardens!, established for many years; garden weed, East Molesey, *A. M. Thompson*!; spontaneous in a greenhouse, Horley, *F. M. Gurteen*!; garden, Limpsfield!
18. S. ESSEX : rubbish tip, Barking!, evidently from garden refuse.
20. HERTS. : pest in garden, Bishop's Stortford, *D. McClintock*.
21. MIDDX. : weed in kitchen garden, Osterley Park, 1900, *A. Lloydell* (OXF) ; now common around Twickenham ; Syon House, Hampton Court, and Chelsea Physic Gardens!; introduced with peat, Shepperton, *P. W. Norman*.
37. WORCS. : garden, Birlingham rectory, Pershore, *D. McClintock*.
54. N. LINCS. : Holton-le-Moor, *D. McClintock*.
56. NOTTS : market garden, Farndon, *R. C. L. Howitt*.
- S. CHANNEL IS. : field, St. Ouen, Jersey, *F. le Sueur*.

Probably much commoner than the above records indicate.

O. DEBILIS Kunth, 1821, in Humboldt, Bonpland, and Kunth, *Nov. Gen. et Spec.*, 5, 236. A plant traditionally known as this grows as a weed in Kew gardens, with *O. corymbosa*. There is a specimen (K) from there dated 1879. It differs from *O. corymbosa* by its smaller (2-3 mm.) bulbils, and in the salmon-pink or brick-red flowers, as compared with the mauve shade of the latter species. The Kew plant is a clone differing from the usual form of *O. corymbosa* (itself no doubt a single clone), but whether it is specifically distinct or is correctly referable to *O. debilis* is doubtful to say the least.

[*O. VIOLACEA* L., 1753, *Sp. Pl.*, 434. Bulb roundish, of lanceolate scales, brown outside; at the base emitting fibrous roots, and occasionally a white tuberous root. *Entire plant glabrous*. *Leaflets* (fig. 2e) obdeltoïd, with a narrow and rather shallow sinus with rounded sides; *with a pair of brown calli underneath at each sinus*, at the end of the midrib, but nowhere else. Inflorescence a simple few-flowered umbel. Sepals rather obtuse, each with a pair of short orange-brown calli at the tip. Petals purplish-rose, 14-20 mm. long. Capsule globose-ovoid, 4-5 mm. long.

United States, in woods and prairies. This side of the Atlantic the plant is much confused with other pink-flowered species. Included in the *B.P.L.* (ed. 2), but I have seen no material to support this; in particular, all material in hb. Druce (OXF) determined as *O. violacea* is either *O. corymbosa* or *O. articulata*. There is no evidence that it has ever occurred in Britain as a wild plant, and it should be removed from the British list. Chevalier (1940, 682) was likewise of the opinion that French records for it were erroneous].

O. LATIFOLIA Kunth, 1882, *Nov. Gen. et Spec.*, 237, t. 467.

Habit of *O. corymbosa*. Bulb (fig. 3b) 1-2 cm. in diameter, consisting of lanceolate scales, the outer ones brown and papery; often with a white translucent conical tuberised root. *Bulbils borne on short horizontal underground stolons* (up to 2 cm. long) *from the base of the bulb*. Petioles 10-30 cm., with a few hairs; *leaflets* (fig. 2c) usually broader than long, 10-25 × 20-45 mm., *obdeltoïd with a wide shallow indentation with straight sides meeting at an obtuse angle, glabrous except for a few cilia at the edge, often purplish beneath, but without any calli*. Peduncles 15-20 cm., ± pubescent; flowers in an *umbel*. Sepals lanceolate, pointed, with two brownish-orange calli at the tip. Petals pink, 8-13 mm. Fruit apparently unknown; the plant spreads vegetatively.

The above description is of what may be called the typical form, which occurs on the continent, in the Channel Isles, and as an occasional garden or nursery weed in various parts of England. It has leaflets with rather long pointed lobes, the whole leaflet having a

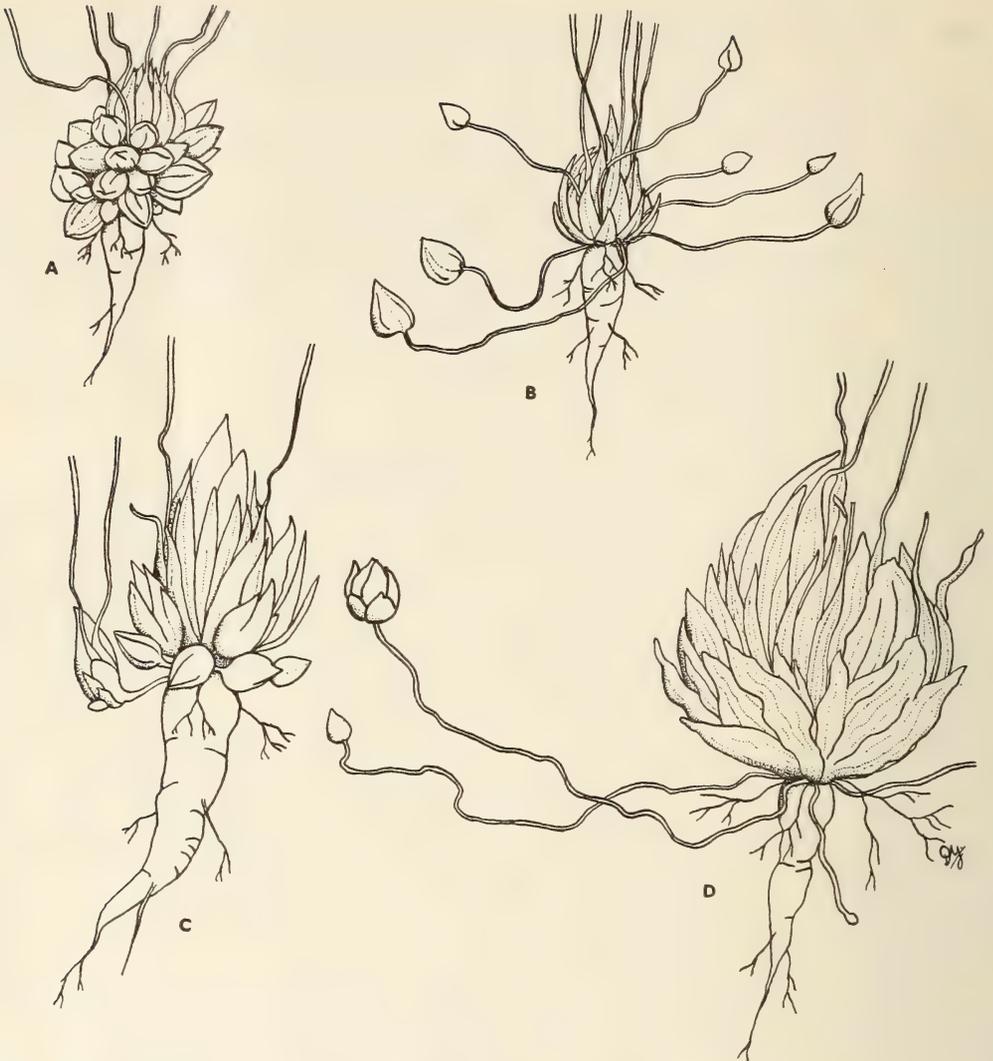


Fig. 3. Bulbs of (A) *Oxalis corymbosa*, (B) *O. latifolia* ("typical" form), (C) *O. latifolia* from Cornwall, (D) *O. tetraphylla*. Natural size. All four are shown with tuberised root, but this is not always developed.

somewhat fish-tailed shape, and comparatively few bulbils on distinct horizontal stolons. The other form, which is now so common in Devon and Cornwall, has *leaflets* (fig. 2D) with a narrower sinus with curved sides, rarely purple underneath, paler flowers, and numerous bulbils which are on short weak erect stalks or almost sessile (fig. 3C). Doubtless these are two different clones; I cannot fit any other specific name to the second form. The last is easily confused with *O. corymbosa*, from which it is distinguished by the wider sinus to the leaflets, which are without any tubercles or dots at the edge and virtually hairless.

Central and equatorial South America, West Indies, etc., in meadows and hillsides. Naturalised as a weed of cultivation in many parts of the world: Mediterranean region, Ceylon, S. Africa. At one time cultivated in gardens in this country. Now a troublesome weed in cultivated ground in market-gardens, glasshouses, and old gardens; uncommon, except in the south-west and in Jersey.

- V.c. 1. W. CORNWALL : weed in cultivated ground, Penzance, 1921, *E. Thurston* (K) ; now in almost every market-garden in the district; in many places around Helston, Camborne, and Falmouth.
2. E. CORNWALL : allotments, Bude, 1943, *D. Stamp* (K); reportedly a pest around Bodmin and Saltash, but I have seen no specimens.
3. S. DEVON : Newton Abbot, *M. L. Bolitho*; Kenn, *A. E. Ellis*; fields, Dawlish, *H. Gilbert-Carter* ; reportedly common in this area.

The above are all the form with rounded leaflets and sessile bulbils. The following are all the " typical " form:

11. S. HANTS : garden weed, Winchester, *D. McClintock*.
58. CHESHIRE : pest in a nursery near Birkenhead, *E. P. A. Jones*.
64. MID-W. YORK : Harewood, 1954, *V. Scott* (BM).
- S. CHANNEL ISLES (Jersey) : field, Bellozane Valley, 1926, *Louis-Arsène* (B.E.C. Distribution) ; fields, St. Ouen, *F. le Sueur*; gardens, St. Helier and Trinity, *idem*; frequent in potato fields, teste *O. Buckle*.

O. TETRAPHYLLA Cavanilles, 1794, *Icones*, 3, 19.

Bulb up to 4 cm. in diameter, of narrow lanceolate striated scales, the outer brown and dry (fig. 3D), often with a white tuberised root at the base; bulbils few, on long flexuous stolons several cm. long. Leaves few, on pubescent petioles; leaflets four, obdeltoid with rounded lobes and a shallow indentation at the apex, 20-25 × 30-40 mm., with thin silky pubescence, sometimes with a purple band across the centre. Peduncles 15-35 cm., strongly pubescent, carrying the flowers in an umbel. Sepals lanceolate, obtuse, with two reddish calli at the tip of each. Petals 20 mm. long, bright rose red. Fruit apparently unknown.

Mexico, on the high plateaux. Naturalised here and there: Simla (India), Java. Occasionally cultivated, but confused with *O. deppei*.

Only in Jersey; introduced in fields in quantity, La Haule, 1926, *Louis-Arsène* (B.E.C. Distribution); still there, also at St. Ouen and Faldouet (Gorey), and in an orchard at St. Aubin, *F. le Sueur*.

The related *O. deppei* Loddiges differs from *O. tetraphylla* in having sessile bulbils, leaves which are scarcely indented at the apex, and larger and more deeply-coloured flowers. Mexico; a well-known garden and greenhouse plant. It does not appear to have become naturalised so far.

Section CERNUAE R. Knuth. Plant with an underground and/or aerial stem from a bulb with inner nutritive scales covered with outer integumental ones.

Inflorescence an umbel. S. Africa.

O. PES-CAPRAE L., 1753, *Sp. Pl.*, 434. *O. cernua* Thunberg, 1781, *Oxalis*, 14. " Bermuda Buttercup."

Bulb ovoid, pointed, 2-4 × 1 cm., with a brown tunic, much like a daffodil bulb, deeply buried up to 25 cm. below ground; with a white contractile tuberised root, and emitting a thin ascending annual underground stem which bears large (5-10 mm.) bulbils along its length and also in a bunch at soil level. Leaves many, springing from the enlarged top of the stem at soil level; petioles lengthening during development up to 20 cm. long; leaflets obcordate, up to 20 × 30 mm., sparsely hairy below. Peduncles 10-30 cm. long, bearing flowers in umbels. Flowers large, bright yellow; sepals lanceolate, 5-7 mm.; petals 20-25 mm. long; flowers trimorphic, but perhaps only one form in this country. Capsule short, not formed in this country. Flowers March-June.

The bulb is annual; each year it shrivels and food reserves pass into the tuberised root, and a new bulb and bulbils are formed later. A lengthy description of the plant's

life-cycle is given by Ducellier (1923). The bulbils are hard and extremely tenacious of life.

Salter (1939) has pointed out that Linnaeus' name is correctly applied to this species and so has priority over the better known epithet *cernua*.

South Africa; said to prefer moist or shady places in its native habitat. Widely naturalised as a weed of disturbed or arid soils, e.g. all around the Mediterranean (a pest in date-groves), Macaronesia, Bermuda, Australia (a pest on sheep and cattle ranges), Uruguay. An account of the plant's spread up to 1910 has been given by Henslow (1910), who asserted that in the northern hemisphere only short-styled plants occurred, and that in consequence it was seed-sterile and spread vegetatively. However, Ducellier, writing in 1923, definitely mentions that in N. Africa the plant sets seed, and so either the barrier (never very strong) to cross-fertilisation between plants of the same style length has been broken down, or else mid- or long-styled plants have been introduced since Henslow's time. The point merits further investigation.

Cultivated as a greenhouse flower in this country; not frost-hardy. A frequent weed in bulbfields in the Scilly Isles, allegedly originating from Tresco Gardens; occasionally in Devon and the Channel Isles.

- V.c. 1. W. CORNWALL : (Scillies); St. Mary's, in many places; St. Agnes, St. Martin's, Tresco, J. E. Lousley. Cf. Lousley (1955).
 3. S. DEVON : Teignmouth, n.d., H. M. Tozer (OXF). Again reported recently, but I have not been able to get confirmation.
 S. CHANNEL IS. : naturalised on a wall at St. Peter's, Guernsey (Marquand 1901, 72); Belcroute Bay, Jersey, 1926, C. Burdo (hb. F. le Sueur); Herm, F. le Sueur.

[*O. SEMILOBA* Sonder, 1860, *Fl. Cap.*, 1, 350. Bulb? Aerial stem often present, pubescent. Leaves from the top of the stem; petioles 6-7 cm. long; leaflets obdeltoïd, deeply lobed, pubescent beneath, 15 × 12 mm. Peduncles about as long as leaves, carrying umbels of 5-15 flowers. Sepals ovate, obtuse, with two brownish calli. Petals 10 mm., retuse, purple. S. Africa, probably as far north as Tanganyika. Apparently not in cultivation, but closely allied to the popular *O. bowiei* Herbert. Reported by Pearsall (1933) as an alien at Polzeath; the specimens (hb. J. D. Grose) are *O. articulata*.]

Section TRIPARTITAE R. Knuth. As *Cernuae*, but inflorescence single-flowered; leaved trifoliolate, petioled. (Sect. *Oppositae* Salter, defined slightly differently).

O. INCARNATA L., 1753, *Sp. Pl.*, 433

Bulb up to 2 cm. long, with a brown tunic, of the size and appearance of a hazel-nut kernel; emitting an *annual stem* that is white and flexuous below ground and *stiff, erect*, and *branching* above ground, 10-20 cm. tall; bearing sessile *bulbils*, 5-10 cm. long, *in the axils*. Whole plant almost glabrous. Leaves opposite, becoming crowded towards the ends of the branches; petioles 2-6 cm.; leaflets delicate, pale green, obcordate, rather deeply lobed, 5-15 × 8-20 mm. Peduncles from the axils, slender, 3-7 cm. long, with a joint with two tiny bracts near the middle. Flowers trumpet-shaped; sepals oblong, acute; petals 12-20 mm. long, pale lilac with darker veins, overlapping. The species does not appear to set seed in this country, but multiplies by the aerial bulbils which drop off when mature.

South Africa, in shady places. Much grown in cottage gardens, and often running wild. In Devon and Cornwall it is frequently naturalised in stone walls and hedgebanks; elsewhere it is found as a relic of cultivation, and being less of a nuisance than other bulbous species it is difficult to decide at what point it is to be considered feral. It is a pretty species, sometimes confused by the tyro with *O. acetosella*, from which it is easily distinguished by its erect stems. The following list of records is probably very incomplete.

- V.c. 1. W. CORNWALL : frequent, also in the Scillies.
 3. S. DEVON : Sidbury, 1936, *J. W. Wyatt* (K); spontaneous in garden, Axminster, *M. L. Bolitho*.
 4. N. DEVON : Weare Gifford, *H. W. Phillips*.
 9. DORSET : in gardens, Swanage, 1933!
 14. E. SUSSEX : site of old cottage, Bishopstone!
 21. MIDDX. : garden, "comes up every year," Hammersmith, 1912, *J. Murison* (K).
 56. NOTTS. : garden weeds, Farndon and Lowdham, *R. C. L. Howitt*.
 74. WIGTOWN : weed in Logan gardens, *R. C. L. Howitt*.
 S. CHANNEL IS. : Guernsey, several places, 1926, *Louis-Arsène* (OXF); Jersey, *D. McClintock*;
 Herm, *F. le Sueur*.

ARTIFICIAL KEY TO SPECIES OF OXALIS WILD IN THE BRITISH ISLES

This key should be used with caution, since other alien species, not included, may be found in the future. It is offered as an aid to tracking down identifications, but they should be checked against the descriptions and if possible against authentic specimens.

A. Flowers yellow.

- B. Plant succulent; stem a thick rhizome; 3 sepals cordate *carcosa*
 BB. Plant not succulent; stem slender or invisible; sepals not cordate.
 C. No aerial stem; bulbils present at base of plant and on underground stem. *pes-caprae*
 CC. Aerial stem present; no bulbils.
 D. Stem short, unbranched; flowers in long cymes; capsule not more than twice as long as broad. *valdiviensis*
 DD. Stems long, branched; flowers in few-flowered umbels or contracted cymes; capsule more than 3 times as long as broad.
 E. Stem rooting at nodes; leaves alternate; stipules obvious, oblong. *corniculata*
 EE. Stem not rooting; leaves whorled or fascicled; stipules inconspicuous or absent.
 F. Peduncles not reflexed after flowering; inflorescence often cymose, with 4 or more flowers; stipules absent. *europaea*
 FF. Peduncles reflexed after flowering; inflorescence umbellate, 2-3 flowered; stipules narrow-oblong, adnate. *stricta*

AA. Flowers pink, pale lilac, or red.

- B. Stem slender, erect, bearing bulbils. *incarnata*
 BB. Stem a \pm procumbent rhizome, sometimes buried.
 C. Rhizome slender, scaly. *acetosella*
 CC. Rhizome woody, over 1 cm. thick, often consisting of oblong or spherical joints. *articulata*
 BBB. No stem; leaves springing from a bulb (or mass of bulbils).
 C. Leaves 4-foliolate. *tetraphylla*
 CC. Leaves 3-foliolate.
 D. Bulb with stipitate bulbils at base; leaflets broadest at or near apex, almost glabrous and without dots on edge beneath. *latifolia*
 DD. Bulb breaking up into a cluster of sessile bulbils at maturity; leaflets broadest at or below the middle, hirsute, with dark dots beneath near the edge. *corymbosa*

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APPENDIX I.

Unpublished vice-county records for *Oxalis corniculata* and *O. europaea*.

Only the earliest record, and in some cases a modern record as well, is given.

O. corniculata

6. N. SOM. : see above, sub var. *microphylla*; Tickenham, 1951, *N. Y. Sandwith* (var. *atropurpurea*).
8. S. WILTS : Salisbury, 1954, R. C. L. Howitt (hb. Howitt).
15. E. KENT : St. Martin's churchyard, Canterbury, teste J. Codrington (var. *atropurpurea*).
33. E. GLOS. : Campden churchyard, 1933, G. W. Hedley (BM).
38. WARWICK : Arbury Hall, 1849, M. Evans (BM).
40. SALOP : under walls, Clun, 1939, J. A. Webb (NMW).
46. CARDIGAN : greenhouse weed, Llanbadarn, 1929, J. H. Salter (NMW); Aberporth, 1951, J. A. Webb (NMW).
49. CAERN. : gardens, Llanfairfechan, 1938, J. A. Young.
57. DERBY : near Kedleston, 1858, F. Mason (BM).
58. CHESHIRE : Thelwall, 1908 (BM).
60. W. LANCS. : Langcliffe Gardens, Lancaster, 1834, S. Simpson (OXF).
61. S.E. YORK : Bempton Lane, Bridlington, n.d., Flintoff (var. *atropurpurea*).
71. MAN : Peel, 1937 ! (hb. Young) (? var. *microphylla*).
85. FIFE : St. Davids, 1845, A. Dewar (NMW).
- H38. DOWN : Singer's nurseries, Newcastle, 1956, teste D. McClintock (and var. *microphylla*).

O. europaea

5. S. SOM. : walls of old town, Minehead, 1905, *A. Loydell* (OXF).
 6. N. SOM. : on tipped earth by laneside, Harter's Hill, Wookey, 1956, *V. S. Summerhayes* (K).
 13. W. SUSSEX : garden weed, Woolbeeding, 1875, *H. E. Fox* (OXF); Henfield Common !
 18. S. ESSEX : Brentwood, 1954, *B. Welch* (BM) (non vidi).
 26. W. SUFFOLK : shrubbery, Nayland, 1893, *J. D. Gray* (BM).
 33. E. GLOS. : garden weed, Cheltenham, 1953, *N. Saunders* (hb. Young).
 38. WARWICK : Arbury Hall, 1853, *M. Evans* (BM) ; garden, Birmingham, ? introduced, 1955, *W. H. Hardaker* (var. *rufa*).
 47. MONTG. : garden weed, Cemmaes, 1901, *G. C. Druce* (OXF) ; Powis, 1955, *H. A. Hyde* (NMW).
 48. MERION. : Ffrith Gate, 1923, *W. C. Barton* (BM etc., see Appendix II).
 49. CAERN. : Bangor, 1919, *G. C. Druce* (OXF).
 55. LEICS. : weed in gardens, Knighton nr. Leicester, 1951, *T. G. Tutin*.
 57. DERBY : "plantations," 1823, *M. Berkeley* (CGE); Matock Bath, 1873 (BM).
 59. S. LANCS. : Hyndburn, Accrington, 1852, *G. F. Dugdale* (BM); several later records.
 69. WESTMD. : nr. Ulverston, 1867, *E. Hawks* (CGE) : garden weed, The Craig, Windermere, 1915, *F. Long* (BM).
 70. CUMBERLD. : garden weed, Near Sawrey, 1956, *M. R. Gilson* (hb. Young) (var. *rufa*).
 74. WIGTOWN : Newton Stewart, 1955, *R. C. L. Howitt* (hb. Young).
 80. ROXB. : introduced, Makerston Wood, 1872, *A. Brotherston* (BM).
 83. EDINB. : garden weed, Liberton, 1908, *R. S. Adamson* (BM).
 87. W. PERTH : gardens, Callendar, teste *D. McClintock* (var. *rufa*).
 H22. MEATH : Pitton House, Drogheda, 1955, *D. McClintock* (hb. Young) (var. *rufa*).

APPENDIX II

Some Distributed Gatherings of the *Corniculata* Group

<i>As labelled</i>	<i>Locality (v.c.), date, collector</i>	<i>Reference</i>	<i>Determination by D.P.Y.</i>
<i>O. corniculata</i>	Par (1), 1908, Mrs. Graham	Watson B.E.C. Rep., 2 , 178 (1909)	<i>O. corniculata</i>
<i>O. stricta</i>	Edmondsham (9), 1914, E. F. Linton	<i>ibid.</i> , 489 (1915)	<i>O. europaea</i>
<i>O. corniculata</i>	Ledbury (36), 1917, S. H. Bickham	B.E.C. Rep., 5 , 215 (1918)	<i>O. corniculata</i>
	Ledbury (36), 1917, S. H. Bickham	<i>ibid.</i>	<i>O. corniculata</i> var. <i>microphylla</i>
<i>O. stricta</i>	Caston (28), 1918, F. Robinson	<i>ibid.</i> 497 (1919)	<i>O. europaea</i>
<i>O. corniculata</i>	Ffrith Gate (48), 1923, W. C. Barton	<i>ibid.</i> , 7 , 379 (1924)	<i>O. europaea</i>
<i>O. stricta</i>	Monmouth (35), 1945, R. Lewis	<i>ibid.</i> , 13 , 155 (1947)	<i>O. corniculata</i>
<i>O. stricta</i>	Rhandirmwyn (44), 1952, I. M. Vaughan	B.S.B.I. Year Book, 1953 , 105	<i>O. europaea</i>
<i>O. europaea</i> var.	Horley (17), 1953, F. M. Gurteen & D. P. Young	Proc. B.S.B.I., 1 , 463 (1955)	<i>O. europaea</i> var. <i>rufa</i>

MINT NOTES

By R. A. GRAHAM

VI. *MENTHA* × *VERTICILLATA* VAR. *TRICHODES* BRIQUET

In 1894 Briquet gave the above name to a mint from Hereford, v.c. 36, which had been sent to him for determination by G. C. Druce, the specimen being now at Oxford. There seems to be no original description of the variety, at any rate in this combination, but a validating text was provided by Fraser (1925, 621), so that the authority for the variety should be corrected to Briquet ex J. Fraser.

During the summer of 1934, Still found a very similar (though not identical) mint in Gower, v.c. 41, and to this, with Fraser's ultimate agreement, he gave Briquet's above name after consulting the Oxford specimen, at the same time giving a full description of the Gower plant (1935, 796-7).

Still, however, was clearly a little uncertain as to the correct status of "var. *trichodes*," and having detected the existence of *M.* × *dalmatica* Tausch var. *trichodes* Briquet [*M. arvensis* L. × *longifolia* (L.) Huds.] he seems to have decided—at any rate for a time—that the Hereford and Gower mints belonged to this hybrid group, indeed his specimens (British Museum, Natural History) are so named. On the other hand he also considered (1938, 663) the possibility of affinity with *M.* × *gentilis* L. (*M. arvensis* × *spicata* L. em. Huds.).

During the autumn of 1956, I visited Gower with Mr. R. M. Harley, and at Park Mill—one of the places where Still recorded it—we refound "var. *trichodes*." As a result the whole matter has been reconsidered.

Firstly, there is no obvious affinity with *M.* × *verticillata* L. (*M. aquatica* L. × *arvensis*), the calyx tube being short and campanulate as opposed to long and tubular as is characteristic of this latter hybrid group. Secondly, insofar as *M.* × *dalmatica* var. *trichodes* is concerned, there is a discrepancy between *folia lanceolata*, *superficie* 4.6 × 1.5-2.5 cm. . . . ; *serratura* . . . *dentibus* . . . *raris, dissitis* . . . as described for this mint (Briquet, 1894, 706) and the broadly ovate (fully developed) leaves, 7 × 4.7 cm., with the many, jagged, closely set serratures of the Gower plant (an interesting feature of the latter is that the upper bract-leaves have extremely few serratures), although if *M.* × *dalmatica* var. *trichodes* was described from inadequate material involving upper bract-leaves only (for which there is no textual evidence) its description might be taken to cover the Gower mint.

The affinity is far more with *M.* × *gentilis* through (1) the campanulate calyx tube with narrow, ± subulate teeth, the whole calyx being normal in shape for mints of the *M.* × *gentilis* group; (2) the sharply multiserrated lower leaves, which strongly resemble those of *M.* × *gentilis*; and (3) the general facies which suggests *M.* × *gentilis* at the same time excluding *M.* × *verticillata*. I have seen no certainly authentic specimens of *M.* × *dalmatica*, but neither the Hereford nor the Gower examples show any characters clearly suggesting *M. longifolia* as a parent. (A secondary point is that this latter species does not seem to grow in Gower). Our mint recedes from normal *M.* × *gentilis* in having largely hirsute calyx tubes and pedicels, rather large corollas, and a general degree of hairiness that exceeds that which is normal for this hybrid. Examples showing a similar

aberrance have been collected at Onich, North Ballachulish, v.c. 97 (Graham, 1947, 33-4). And the pungent, spearminty flavour, which characterises the hybrids of *M. spicata*, is largely absent in the Gower plant.

There can, I think, be no doubt that "*M. verticillata* var. *trichodes*" is in fact merely an aberrant form or sport of *M. × gentilis*, and the affinity can be taken even further in that there occurs in the Bishopstone Valley, east of Park Mill, a form of *M. × gentilis* known as var. *vesana* Lej. & Court., which is characterised by jaggedly serrated leaves. We were unable to re-find this variety, but herbarium specimens show the lower leaves to be extremely like those of "var. *trichodes*." Still apparently found both growing together in the Bishopstone Valley, and it is significant that he reports difficulty in telling them apart in the field. The most probable status of "var. *trichodes*" is therefore a sport or aberrant form of *M. × gentilis* var. *vesana*. Root of the Gower "*trichodes*" has been taken to grow under observation.

The Gower examples differ from the Hereford plant in having a rather shorter calyx tube and considerably shorter cilia on the calyx teeth: but the two should be regarded as essentially the same sort of mint.

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MINT NOTES

by R. A. GRAHAM

VII. MENTHA × MAXIMILIANEA F. SCHULTZ IN BRITAIN.

The occurrence in Britain of *M. × maximiliana* F. Schultz* (*Mentha aquatica* × *rotundifolia*) has been suspected since 1950 when two specimens which seemed to be this came to my notice in the herbarium of Cambridge University. For one reason or another the matter was not pursued at the time, but has been recently reconsidered following the discovery by Dr. J. K. Morton of fresh material of this rare hybrid in the Brixham area of South Devon, v.c. 3. The Cambridge specimens have been re-examined. I have seen the holotype (at Geneva, with a photograph at Kew and an isotype at Manchester) of *M. × maximiliana* var. *baileyi* Briquet (1889, 68)—a mint whose existence seems to have remained un-noticed by those who have compiled lists of British plants despite the fact that it originated from Guernsey in 1867—which would seem to constitute yet another British record for the *M. × maximiliana* group: but the specimen is merely a rather hairy water mint [*M. aquatica* L. var. *hirsuta* (Huds.) Huds.] (Graham 1954, 112) whose original identification must therefore be amended. In fact, it shows no indication whatsoever of *M. rotundifolia* in any of its characters.

The acceptable records for Britain of *M. × maximiliana*, so far as I have yet detected them, are in their chronological order as follows:—

1. Orchard, Tresgoddern, Cornwall, (? v.c.), *Borrer* s.n. (Cambridge)
2. Damp meadow, Chyvogue, Perranarworthal, W. Cornwall, v.c. 1, 1911, *Hamilton Davey* 1319 (Cambridge)
3. Man Sands, Brixham, S. Devon, v.c. 3, 1955, *J. K. Morton* (herb. J. K. Morton 4406; herb. R. A. Graham 4730)

Among Schultz' specimens in the Kew herbarium, No. 115 comprises two sheets which are probably isotypes of *M. × maximiliana* (i.e. var. *maximiliana*), while No. 116 similarly comprises isotypes of *M. × maximiliana* var. *exserta* F. Schultz (1854b, 36) (= var. *weissenburgensis* F. Schultz ex H. Braun, 1890, 412). *M. × maximiliana* var. *schultzei* Boutigny ex H. Braun (1890, 412) appears from a specimen, also at Kew, which may be its holotype, to be probably a short-leaved, short petiolate peppermint (*M. × piperita* L. agg.) and will not be further considered here.

The type description of *M. × maximiliana* (Schultz 1854a, 225) is followed by an apparently later description (Schultz 1854b, 34) with, in both cases, additional German text that is rather more informative than the Latin. Schultz 115, from the Lower Rhine, can be described as follows:—*Stem* 50-60 cm. tall, branched, covered with simple, woolly hairs. *Leaves* broadly ovate, sometimes ± rounded, up to 5 × 3.2 cm., apically acute or

*It is possible that *M. pyramidalis* Tenore (1811, 34) may antedate *M. maximiliana* as the correct binomial for this hybrid group, as has been most recently suggested by Litardière (1955, 42). I have seen two of Tenore's Corsican specimens of *M. pyramidalis*, neither of which are necessarily types but both of which although differing from each other may nevertheless be hybrids of *M. aquatica* with *M. rotundifolia*. But the matter does not rest there, as it is first necessary to establish the relationship of the latter species with the apparently closely allied *M. insularis* Req. ex Gren. & Godr. (1850, 649) which, as well as *M. rotundifolia* and *M. aquatica*, grows in Corsica whence *M. pyramidalis* was first described. It is not yet certain that *M. pyramidalis* may not more correctly apply to a hybrid of *M. aquatica* with *M. insularis*. Apart from this, there are certain other binomials whose claim to priority over *M. maximiliana* should be examined, but as the uncertainty regarding *M. pyramidalis*—which seems to be the earliest possible name—remains for the time being, it has been thought advisable to fall back on a binomial about which there is no doubt as to validity and applicability [for a similar view, see Briquet (1891, 63)].

obtuse, basally truncate to cordate, sometimes asymmetrical with up to 5 mm. discrepancy; greenish-white due to white tomentum on both faces but more sparsely hairy above and not thickly felted below; serratures rather jagged, irregular in size, \pm outward-directed, up to 9 on each side: upper leaves tending to be round. *Petioles* short, not exceeding 5 mm. in length. *Inflorescence* a terminal spiciform raceme, 2.6-5 cm. long and 1.2-1.4 cm. broad at maturity, interrupted below. *Corolla* and *calyx* very hirsute with \pm patent white hairs.

This mint is from its outward appearance a reasonably obvious hybrid of the two putative parent mints: the ovate leaves, terminating in a point, suggest *M. aquatica*, while their very short petioles, the broad width in ratio to the length, and the tendency of the upper leaves to roundness suggest *M. rotundifolia*: the inflorescence is \pm intermediate between the capitulum of *M. aquatica* and the spiciform raceme of *M. rotundifolia*: further, a comparison of the calyx and corolla measurements of this putative hybrid with average figures of its putative parent species shows an additional intermediate state, as the following table indicates.

	<i>M. rotundifolia</i>	<i>M. × maximiliana</i> (Schultz 115)	<i>M. aquatica</i>
Calyx teeth	0.85 mm. long	c.1 mm. long	1.25 mm. long
Calyx tube	1.1	c.2	2.75
Corolla overall	2.15	3.75	6.2

Var. *exserta*, from the same district, is a very similar mint, certainly unworthy of taxonomic separation from var. *maximiliana*. It recedes a little further towards normal *M. aquatica* in having slightly broader racemes (up to 1.5 cm.), which are also slightly shorter and more irregularly interrupted into component, \pm capitate verticils: the leaves, too, are rather longer for their width (4.5 \times 2.4 cm.). But these differences are of no importance.

Of the British examples of *M. × maximiliana* seen—and all differ from each other in various respects—only the Man Sands material (see Fig. 1) nearly approaches Schultz' specimens, the affinity being in fact very close to var. *exserta* but the calyx of our mint is rather longer (4 mm. overall), likewise the petioles (up to 1.8 cm.). Fortunately both putative parents grew alongside, thus a comparison of the flower characters of all three is possible, as shown below.

	<i>M. rotundifolia</i> (Morton 4405; Graham 4655)	<i>M. × maximiliana</i> (Morton 4406; Graham 4730)	<i>M. aquatica</i> (Morton 4404; Graham 4654 a. & b)
Calyx teeth	0.5 - 1 mm.	1.25 mm.	1.25 mm.
Calyx tube	1.25 - 1.6	2.75	3.0
Corolla overall	4.0	5.0	7.0
Raceme maximum width	11.0	18.0	22.0

The two examples at Cambridge are outwardly very different from each other and from the forms of this hybrid already discussed, from which they differ in one particularly interesting feature in that they both bear some branched hairs (which are characteristic of *M. rotundifolia* but not of *M. aquatica*) among the mass of simple ones. In the Perranarworthal plant there is some resemblance to *M. aquatica × longifolia* (*M. × dumetorum* Schultes = *M. palustris* Sole non Mill.) but unlike this latter the leaves are sessile or almost so, which, with their broadly ovate shape and softly tomentose undersurfaces, suggests the influence of *M. rotundifolia*.

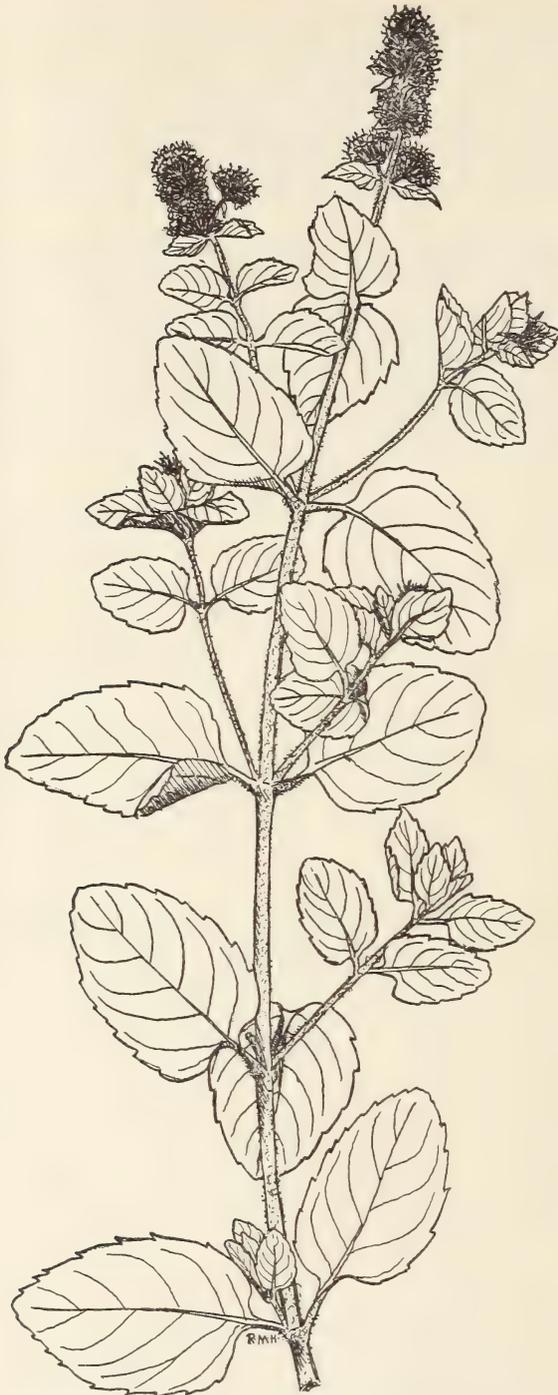


Fig. 1. *Mentha* × *maximiliana* F. Schultz, × $\frac{3}{4}$, from herb. R. A. Graham No. 4730 (Man Sands, v.c. 3).

The Tresgoddern specimen is a reasonably obvious hybrid of the two suggested parents, having ovate, very obtuse, shortly petiolate leaves of which the lower tend towards terminal roundness, and a \pm spiciform-racemose inflorescence which seems to be composed of many, small, closely-set capitula, neatly suggesting an intermediate state.

So far as British material is concerned, *M.* × *maximiliana* is apparently very rare,

and, clearly, very variable. Indeed the variability is such that it becomes extremely difficult to indicate reliable characters whereby this hybrid may be detected. Outwardly, an intermediate appearance seems to be the best guide, and bearing this in mind the only British mints with which *M. × maximiliana* could normally be confounded are *M. × piperita* forma *hirsuta* (J. Fraser) R. A. Graham (1951, 32) and *M. × dumetorum*. It can be told from both by having leaves broader in ratio to their length, and sometimes sessile (a feature lacking in either), from the first by the lack of pepperminty flavour (insofar as fresh material of the Man Sands plant has indicated), and in certain cases by the presence of branched hairs. For further distinctions from hybrids of the *M. aquatica × longifolia* group, but referring to continental material, see Schultz (1854a, 226) and Briquet (1891, 62).

I refer now to two mints which may possibly be forms of *M. × maximiliana*. The first of these was found at Sennen Cove, West Cornwall, v.c. 1, by Mr. O. Polunin in 1955 (herb. R. A. Graham 4725), which although outwardly seeming to be a white-shaggy form of *M. aquatica* is worth further study in order to be more certain of any possible hybrid origin. The second was found during 1954 in Bone Valley, Penzance, v.c. 1, by Miss B. M. Sturdy, and has been under observation in my garden for two seasons. It has been exhibited at our annual Exhibition Meeting as *M × maximiliana*, and as such has been privately distributed (herb. R. A. Graham 4918). It is a capitate mint, very similar in this respect to *M. aquatica* as which most collectors would probably dismiss it in the field; indeed it reflects the highest credit on Miss Sturdy that she perceived certain unusual features in it and thought it worth submitting. It differs from normal *M. aquatica* in the leaves, some of which are terminally rounded and whose bases are remarkably cordate with rounded lobes enclosing a basal sinus up to c. 5 mm. deep, while some of the bract-leaves are \pm sessile. These features suggest the influence of *M. rotundifolia*. The capitula appear to be normal for *M. aquatica*, the flowers having exerted stamens with fertile pollen, and producing a large quantity of viable seed which appears to be identical with that of a normal *M. aquatica*, and of which a high percentage was successfully germinated by Mr. R. M. Harley (surviving the winter, the seedlings promptly died off in the spring)*. The calyx, however, is short for this species (3—3.2 mm. long overall), with short teeth (0.75—1 mm. long). The original specimen sent to me gave, owing to the terminally rounded, basally cordate leaves, a strong look of the influence of *M. rotundifolia*, which a glance at the short calyces seemed to confirm. Recently I have examined further examples of *M. aquatica* from various sources, among them a specimen from Folkestone, v.c. 15, which had a nearly exact resemblance to some of the less extreme forms of the Bone Valley plant; indeed the affinity was so great that it was impossible to separate one from the other on any good diagnostic character. This prompted further examination of the Bone Valley mint, and it transpired that the features which seemed to savour of *M. rotundifolia* occurred now and then in normal *M. aquatica*, and that the original Bone Valley specimens were merely forms wherein these several features were all present giving, as a result, a highly deceptive appearance. On this, it would appear that the plant is merely *M. aquatica*. But the chromosomes have been counted, giving a figure $2n=108$ (*M. aquatica* $2n=96$; *M. rotundifolia* $2n=24$), which, since British *M. aquatica* appears to be constantly $2n=96$, is a little surprising. If we assume that this mint is indeed a hybrid of the *M. × maximiliana* group, the figure $2n=108$ can be explained as resulting from the backcross of an amphidiploid hybrid with the *M. aquatica* parent, and it is true that the general appearance of the plant offers reasonable grounds for accepting this—including the production of seed which might be due to the influence of amphidiploidy. But owing to the inescapable fact that this unusual mint agrees fundamentally with *M. aquatica*, but with

*It is worth mentioning that Mr. Harley also, but at low percentage, germinated seed obtained from *M. × niliaca* Juss. ex. Jacq. var. *villosa* (Huds.) Druce, and "*M. × niliaca* var. *sapida* (Tausch) Briq." but both unfortunately suffered the same fate.

certain characters in rather extreme form, to the extent that it appears to be impossible to distinguish it apart, and bearing in mind that in its habitat it occurs with many other examples of apparently normal *M. aquatica* into which its characters merge (*M. rotundifolia* is, so far as I have observed, absent from the immediate neighbourhood of the plant), I believe that my original determination must be amended to one of *M. aquatica* L. (agg.), at any rate until further investigation may satisfactorily prove otherwise.

I am greatly indebted to Professor Baehni, Dr. S. M. Walters, Dr. E. F. Warburg, and to the Curator of the herbarium at Naples for loan of specimens. Foreign material has been photographed, and prints are at Kew. I am also very grateful to Mr. R. M. Harley for the accompanying drawing and for much helpful assistance, and to Dr. J. K. Morton for counting the chromosomes.

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Since writing the above account, there has come into my hands from the Manchester herbarium a specimen which provides adequate evidence, by analogy and inference, for a more definite pronouncement on the Bone Valley mint. This specimen is part of cultivated material which was distributed through the B.E.C. and the Watson Exchange Club under the name *M. pubescens* Willd. var. *palustris* "Sole" (= *M. × dumetorum* Schultes), the root having originated from St. Colomb Minor, near Newquay, v.c. 1; and early comments on its origin, etc., can be read in the Reports of both these Exchange Clubs for 1908. In the example seen, the leaves are too like those of the Bone Valley mint – even to the extent of having basal sinuses – to be distinguishable, and an essential similarity can be accepted. But the inflorescence is not a capitulum, as in the Bone Valley mint, but a stout spiciform raceme, c.7 cm. long × 2 cm. broad, which suggests a hybrid origin, with the influence of *M. aquatica* in its breadth and a "spicate" species in its elongation. It is difficult to accept affinity with *M. × dumetorum*, as there is no character reliably indicative of *M. longifolia* in its appearance, and it is far more likely, from the leaf shape, that the "spicate" parent mint is *M. rotundifolia*. The floral measurements are intermediate between *M. aquatica* and *M. rotundifolia*, viz., calyx tube 2.5 mm. long, calyx teeth 1.5 mm. long, and corolla 5 mm. long. The specimen is rather young, but there is some seed which appears to be developing. As in the Bone Valley mint, there appear to be no branched hairs.

It is reasonable to infer from the leaf characters of this example, and from the fact that its floral measurements, although not exactly agreeing with those of the Bone Valley mint (some variation is inevitable), still suggest intermediacy between *M. aquatica* and *M. rotundifolia*, that both the Bone Valley and St. Colomb Minor mints are essentially the same, with the difference that the inflorescence, in the one case, suggests strongly one parent (*M. aquatica*) while, in the other, its appearance suggests a hybrid between this species and *M. rotundifolia*. It will be remembered that the chromosome number of the Bone Valley mint supports the idea that it is a hybrid of these two mints, and, although no such guide is at hand to help in assessing the origin of the St. Colomb Minor mint, I believe that the form of the inflorescence of the latter is probably one which that of the Bone Valley mint can attain by normal variation. By analogy, a capitate form of *M. × dumetorum*, in my garden see 1953, *B.S.B.I. Year Book*, 1953, p. 109), produced "spicate" inflorescences during the summer of 1955, and has since reverted to the capitate form again. Whether this can apply to the Bone Valley mint, can only be known by observation, and the same applies in a reverse sense in the St. Colomb Minor material. This much can be said, that the inflorescence of the latter is such as would be expected if the Bone Valley mint were to show, in its inflorescence, the hybrid origin which its leaves and chromosome number suggest. On the evidence, it seems that both these mints are *M. × maximiliana*, and that both are essentially the same sort of hybrid which, very different in appearance from Schultz' types and from the Man Sands material, may later come to be regarded as representing a distinct nothomorph.

A BIOSYSTEMATIC STUDY OF SOME *GLYCERIA* SPECIES IN BRITAIN*

3. BIOMETRICAL STUDIES

By MARTIN BORRILL

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INTRODUCTION

The British representatives of section *Glyceria* are paludal species, they occupy a wide range of habitats and are occasionally found growing together (Hubbard, 1942); nevertheless each shows slightly different ecological tolerances. *G. declinata* ($2n = 20$) can grow in turf likely to be trampled and to dry out in summer. *G. fluitans* ($2n = 40$) is ubiquitous, and like *G. declinata* is able to flourish in both acidic and base-rich soils, whereas *G. plicata* ($2n = 40$) is intolerant of acid soils. Both *G. plicata* and *G. × pedicellata* ($2n = 40$) are stoloniferous, forming large stands in shallow water. The hybrid flourishes in swift flowing water.

Because these grasses are restricted to paludal habitats they are divided into many small, spatially isolated, local populations which occur in ponds, on mudbanks, or at the bends of rivers and streams. Many populations have minor differences in floral morphology, and they are often very distinct vegetatively. Examples are: a luxuriant form of *G. declinata* sometimes found in humus-rich ponds (Hopedale, Stafford, H.506)[†], a form of *G. fluitans* in which the palea-apex greatly exceeds the lemma (Broad oak, Monmouth, H.426 and in Herb. Kew), and the *triticea* forms or varieties of *G. fluitans* and *G. plicata*, characterised by simple spiciform inflorescences (H.460, H.423).

Previous authors (Hubbard, 1942; Lambert, 1949; Jungblut, 1953) regard the varieties as ecological forms dependent on habitat conditions and changing with them, and they are not chromosomal races (Borrill, 1956b). Consequently some of these forms were compared in the same environment to see whether their phenotypic differences had a genetic basis.

MATERIAL

Seeds were collected from 15 populations, the characteristics of which are shown in Table 1. The limits of individual plants were explored in an attempt to ensure that seed was not derived from one clone. The plants raised from this seed formed samples of the potential biotypes in the populations (Baker, 1953). Each will be referred to as a 'race.' The plants were grown in the same environmental conditions from germination, namely 960 ft.-candles fluorescent light for 17 hours at a mean temperature of 28.5°C., with 7 hours darkness at a mean of 18.5°C. When the fourth leaf in each species appeared, a randomised block with three replicates was planted. The blocks were irrigated with a lawn spray.

DATA RECORDED

All the measurements were based on homotypes, i.e., organs of similar position and maturity (Pearson, 1901; Gregor *et al.*, 1936). A list of those used is given in Table 2.

* 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 of Leicester.

† Specimen citations are given in the following form: H.506 = specimen No. 54506 in Herb. Univ. Leicester.

TABLE 1. Seed parents for garden trial.

Herb. No.	Race	Locality	Vice County	pH	Habitat	Morphology			Anthers	
						Habit	Leaf	Culm		Lemma
G. <i>declinata</i> 468	A	Malham Beck	64	7.6	Mudbanks in limestone stream	Small, rather spreading	Narrow, tapering towards apex. Pale green, purplish on sheath	Short, slightly curved	4.0—4.5 mm., 3-toothed, occasionally lobed at spikelet extremities, nerve tips purple	0.75—1.00 mm. purple
	B	Malham Cove	64	7.3	Mudbanks at foot of limestone cliff	Large, prostrate, 'cup' type	Rather narrow, scarcely tapering, apex abruptly contracted, mucronate, slightly glaucous	Few, of medium length, slightly curved	4.0—4.5 mm., usually 3-toothed, sometimes obscurely lobed	0.75—1.00 mm. purple
413	C	Ulverscroft	55	4.6	Gravel bed of small stream	Large, erect	Broad, more or less tapering, occasionally slightly mucronate at apex	Many, long, erect and more or less curved	4.0—4.5 mm., conspicuously 3-toothed	0.8—1.25 mm. purple
427	D	Cadgwith	1	—	Quarry pond at cliff top	Large, spreading	Somewhat tapering, occasionally slightly mucronate at apex, more or less glaucous	Few, long, curved	4.0—4.5 mm., somewhat acute at apex, 3-toothed	Up to 1.00 mm. purple
506	E	Hopedale	39	5.4	Muddy pond rich in humus	Very large, massive	Very long and broad, scarcely tapering, apices contracted, abruptly mucronate	Long, spreading, curved - ascending, thick	About 4.0 mm., 3-5 toothed, sometimes lobed	0.8 to 1.0 mm. yellow or purple
G. <i>plicata</i> 400	F	Fulborn	29	8.2	Chalky soil, bank of clear chalk stream	Slender, stiff, erect, bushy	Rather small, tapering, often folded, rather dark green for species	Many, stiff, and straightly erect	4.0—4.5 mm., rounded or obscurely lobed at apex	1.0—1.25 mm. yellow
	G	Breedon	55	6.9	Gravel bed of small stream	Large, spreading	Medium size, more or less tapering	Few, long, lax, spreading, erect	4.0—4.25 mm., rounded or more or less lobed	ca. 1.25 mm. yellow
444	H	Wistow	55	5.3	Edges of pond in marl pit	Erect, bushy	Long and broad, tapering towards apex	Many, long, stiff, straightly erect	4.0—4.5 mm., rounded or lobed, nerves purple-tipped when in fruit	1.0—1.25 mm. yellow

TABLE I.—continued. Seed parents for garden trial.

Herb. No.	Race	Locality	Vice County	pH	Habitat	Morphology				
						Habit	Leaf	Culm	Lemma	Anthers
<i>G. plicata</i> 466	I	Malham	64	7.2	Freshet on limestone	Small, compact	Slender, short, tapering and often folded, purplish on leaf sheaths	Few, geniculate ascending-erect	3.5—4.0 mm., obscurely lobed or 3-toothed, scarlet-bordered	ca. 1.0 mm. purple
423	J	Wittering	32	6.2	Small spring on limestone	Small, spreading	Medium size, more or less tapering	Rather short, spreading-ascending	4.0—4.5 mm., more or less rounded, black-tipped in fruit	1.0—1.25 mm. yellow
<i>G. fluitans</i> —	K	Breedon	55	6.9	Bed of canal, mud rich in humus	Stiff, ± erect	Medium size, rather stiff, and often folded, dark green	Spreading, ascending, to erect	ca. 6.0 mm., apices acute and more or less sinuous	ca. 2.0 mm. purple
454	L	Ulverscroft	55	4.3	Muddy ditch	Large, rather spreading	Long, lax, often flat, rather pale green	Long, straight-ascending	6.0—6.5 mm., noticeably exceeded by palea points, apex acute often lobed	2.0—2.5 mm. yellow
437	M	Loddington	55	5.5	Wet place in fields at Loddington Reddish	Large, spreading	Long and more or less folded, later flat. Rather lax, pale or medium green	Long, straight-ascending	6.0—6.5 mm., usually exceeded by palea points, apex acute and smooth	2.0—2.5 mm. yellow or purple
490	N	Acle	27	4.1	Trodden ground by dike	Small, slender	Stiff, short, often folded and dark green	Few, short	6.0—6.5 mm., equals length of palea, acute, irregularly lobed, nerve-tips blackish	1.5—2.0 mm. yellow or purple
475	O	Acle	27	3.9	ca. 30 cm. water in dike	Very large, coarse, and stiff	Medium size, stiff, often folded, dark green, blackish on sheaths	Very long, woody, nodally rooting	5.5—6.0 mm., more or less equals palea, apices smooth or slightly sinuous, acute	ca. 2.0 mm. purple

TABLE 2.

Details of the homotypic characters.

Measurements averaged to obtain the mean value for each plant. *G. declinata*, *G. fluitans* and *G. plicata* :

Lemma length	= Lemma of supra-basal floret in terminal spikelet of major pedicel at each node on the first three culms.
Florets per spikelet	= Number of florets in each spikelet measured.
Spikelet length	= Length of each spikelet measured.
Culm length	= Length of the three longest culms.
Panicle length	= Length of the panicle in each culm measured.
Number of internodes	= The internodes of each panicle.
Emergence date	= Interval from germination up to the emergence of the second culm.
Leaf length	} = Length and width of the three longest leaves on the three longest culms and tillers (The averages of the culm leaves and tiller leaves used separately).
Leaf width	
Leaf index	= Ratio $\frac{\text{Mean leaf length}}{\text{Mean leaf width}}$
Number of culms	= Total number of culms on the plant.
Number of shoots	= Total number of shoots on the plant.
Dry weight	= Weight of the whole plant excluding the root system.
For <i>G. plicata</i> only:	
Major tillers	= Number of long stolons on the plant.
Major tiller length	= Length of these stolons.
Crown tillers	= Number of vegetative shoots at the crown of the plant.
Secondary tillers	= Number of tillers borne on each culm.
Tiller number	= Number of tillers borne on each stolon.

In the case of the consistently stolon-forming *G. plicata*, with both heading and non-heading plants, these two forms were considered separately as follows :—

In the heading plants the numbers of short vegetative shoots at the centre, and of secondary tillers borne on the culms; *in the non-heading*, the number and length of the long stolons, and number of short vegetative shoots at the centre, and of secondary tillers borne on the stolons.

At the end of the experiment, the plants themselves were lifted (leaving the roots in situ), partially dried and stored; before measurement, leaves were floated on a detergent solution to restore their normal size.

The data were subjected to an analysis of variance, and the homotype-means for all the races are shown in Table 3, where differences significant at $P = 0.01$ are indicated.

DISCUSSION

Highly significant differences were shown by the population samples grown in the same environment (Table 3); consequently there are genetic differences between them. In general, they retained the characteristic morphological features of the parental populations.

The numerical differences between the homotypes give precision to visible variations between the races. Ideographs (Fig. 1), based on the suggestion of Anderson (1949), have been prepared for each population sample, consisting of (1) a base representing the vegetative part of the plant and (2) an erect portion showing the culm, with leaf and spikelet homotypes. The height of the leaf from the base is proportional to the interval between sowing and heading.

TABLE 3.
The occurrence of significant differences between race means.

Character	Mean values				
	A	B	C	D	E
<i>G. declinata</i>					
Florets per spikelet	6.27	(7.87)	(7.09)	(7.37)	(7.73)
Spikelet length (mm.)	<u>(15.0)</u>	16.4	14.3	(15.2)	<u>(15.4)</u>
Culm length (cm.)	47.6	(52.9)	<u>(52.4)</u>	(50.5)	(51.7)
Panicle length (cm.)	[23.2]	(27.5)	24.2	[24.0]	(28.0)
Number of internodes	10.5	[11.3]	(11.8)	[11.2]	(11.8)
Emergence date	29/7	5/8	27/7	20/7	1/8
Leaf length (mm.)	(77.7)	96.2	(72.7)	(76.3)	105.4
Leaf width (mm.)	[5.91]	(6.66)	[5.99]	(6.43)	[7.09]
Leaf index $\frac{\text{Length}^1}{\text{Breadth}}$	13.0	[14.5]	(12.0)	(11.9)	[14.7]
Total culms	(15.1)	(12.9)	41.2	24.9	(11.6)
Total shoots	154.0	175.0	(116.0)	<u>(111.0)</u>	<u>(132.0)</u>
Dry weight (gm.)	<u>(24.2)</u>	37.5	<u>(30.7)</u>	17.1	<u>(28.8)</u>
<i>G. plicata</i>					
	F	G ²	H ²	I ²	J
Florets per spikelet	8.09	—	—	—	8.61
Spikelet length (mm.)	16.3	—	—	—	17.8
Culm length (cm.)	69.3	—	—	—	79.4
Panicle length (cm.)	(24.9)	—	—	—	(24.7)
Leaf length (mm.)	[104.3]	(142.9)	165.2	(139.5)	[109.5]
Leaf width (mm.)	(6.20)	7.45	9.25	(6.18)	(6.25)
Leaf index $\frac{\text{Length}^1}{\text{Breadth}}$	(16.0)	18.9	(17.7)	22.4	(17.3)
Number of culms	21.6	—	—	—	42.3
Total shoots	92.1	(165.9)	279.9	236.3	(153.0)
Dry weight (gm.)	31.2	(53.1)	80.3	(50.0)	(52.8)
Total major tillers	—	(12.8)	18.9	(12.3)	—
Length major tillers	—	90.6	139.0	60.1	—
Crown tillers	<u>(51.8)</u>	(62.3)	<u>(73.3)</u>	123.9	<u>(69.6)</u>
Secondary tillers	23.4	—	—	—	41.3
Mean tiller number	—	(7.14)	<u>(10.33)</u>	(8.48)	—
<i>G. fluitans</i>					
	K	L	M	N	O
Lemma length (mm.)	[5.86]	(6.39)	(6.24)	(6.42)	[5.73]
Florets per spikelet	10.10	11.20	12.42	9.16	8.48
Spikelet length (mm.)	(24.5)	(25.9)	(25.4)	20.80	18.0
Culm length (cm.)	(62.7)	75.3	(64.8)	59.30	71.9
Panicle length (cm.)	[29.5]	[27.1]	[28.0]	22.90	<u>[31.6]</u>
Number of internodes	9.68	—	—	9.50	11.64
Emergence date	17/7	8/8	14/8	12/7	18/7
Leaf length (mm.)	(126.6)	217.5	197.5	(127.5)	158.5
Leaf width (mm.)	<u>(6.33)</u>	[7.99]	[7.49]	(6.65)	<u>(7.03)</u>
Leaf index $\frac{\text{Length}^1}{\text{Breadth}}$	[20.1]	(27.1)	(26.3)	[19.1]	22.8
Total culms	24.3	[8.0]	[8.14]	(14.84)	(14.42)
Total shoots	(97.1)	[76.7]	[84.9]	55.4	(105.1)
Dry weight (gm.)	21.1	(18.0)	(16.2)	(16.0)	26.4

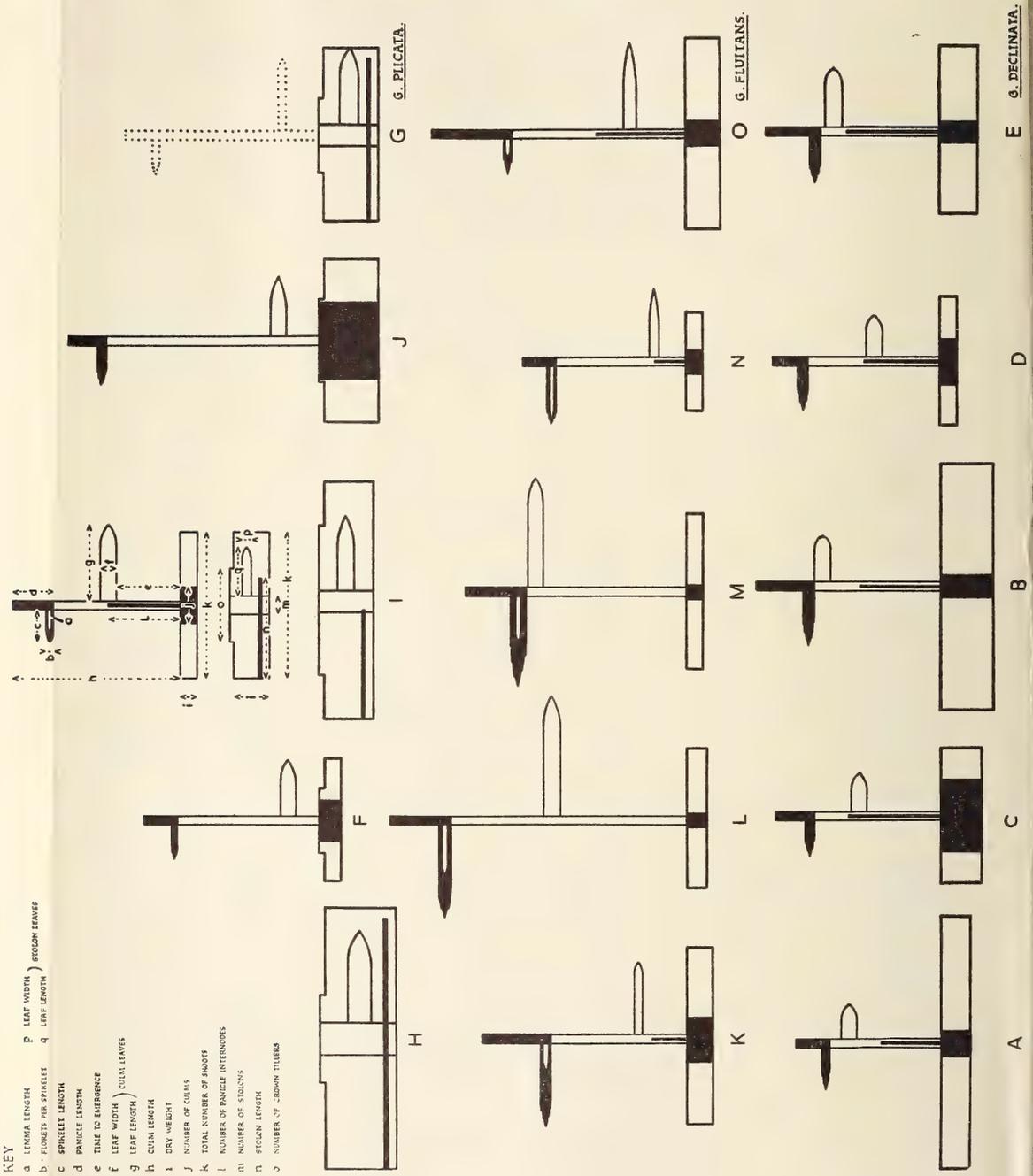
Unbracketed figures differ from all others. Figures in like brackets similar. Bracketed figures underlined or barred differ. All differences significant at $P = 0.01$.

1. A 't' test. 2. Plants almost or entirely non-heading.

Fig. 1.

IDEOGRAPHS OF FIFTEEN GLYCERIA POPULATIONS

EXPLANATION IN TEXT



KEY

- a LEMMA LENGTH
- b FLORETS PER SPIKELET
- c SPIKELET LENGTH
- d PANICLE LENGTH
- e TIME TO EMERGENCE
- f LEAF WIDTH
- g CULM LENGTH
- h LEAF LENGTH
- i DRY WEIGHT
- j NUMBER OF CULMS
- k TOTAL NUMBER OF SHOOTS
- l NUMBER OF PANICLE INTERNODES
- m NUMBER OF NODES
- n STEM LENGTH
- o NUMBER OF BROWN TILLERS

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
G. DECLINATA

The main differences between the populations are shown in Fig. 1. In *Glyceria declinata* and *G. plicata*, plant bulk is the main feature, measured by dry weight and number of culms and shoots (i, j and k); floral differences are less pronounced.

Race E of *G. declinata* retained the luxuriant habit characteristic of the parent population, and, with race B, is a distinct type characterised by large vegetative and floral parts. The leaves are long, broad and conspicuously mucronate (Fig. 3), those on the vegetative shoots being significantly longer than those on the culms, as shown below.

Analysis of variance, leaf morphology

Race	Character	Type of shoot	Mean (mm.)	Diff. (mm.)	Minimum significant numerical difference (P = 0.01)
B	Leaf length	Tiller	10.71	1.09	0.471
		Culm	9.63		
E	Leaf length	Tiller	11.75	1.34	0.865
		Culm	10.41		

In *Glyceria plicata*, grown, like the other species, without low-temperature treatment, two races headed, two did not, and race G was intermediate in behaviour. This is interesting, since Lambert (1949) considered that delay of flowering until the second season distinguished *G. plicata* from the other British species of section *Glyceria*. In fact, the position is more complex.

Fig. 1 shows that the non-heading plants made more growth and that races H and I are opposite in habit, the former being very spreading with long, broad leaves (Fig. 3) and the latter with a tufted crown and short stolons. A difference was seen between the parents and offspring of race H. In the field these were slender, erect, floriferous plants resembling race F. The larger size and increased vigour of the progeny are due to suppression of heading.

Homotype correlation was studied by means of scatter diagrams. An example is the relation between spikelet length and number of florets in *Glyceria fluitans*. Fig. 1 and the histograms in Fig. 2 show that these are closely correlated, whereas lemma length is independent.

The homotypes fall into three correlation groups (Fig. 1) :—

1. Those concerned with the size of the vegetative parts of the shoots, i.e. culm length, panicle length, number of internodes per panicle, leaf length, leaf width.
2. Those providing a measure of plant bulk i.e. dry weight and number of shoots.
3. The spikelet characters.

Quite strict correlation is the rule within a population but there are departures from this when passing from one population to another. The fact that populations tend to have independent centres of variation enhances their phenotypic distinctness. A similar situation has been described in *Panicum virgatum* by Nielson (1944).

In *G. fluitans* (Fig. 1) the differences between the races are in spikelet — (Fig. 2), leaf — (Fig. 3), and culm — length, in contrast to the other species, where bulk was most important. Races L and M are similar with spreading habit, long, lax, flat, pale green leaves, and large spikelets. Race N, at the other extreme, was compact, with short, stiff,

dark green and more or less folded leaves, and short spikelets with very long lemmas. One local population sample, an extreme form of *G. fluitans* var. *triticea* from an acid pool at Great Close Mire, Malham, Mid West York (H.460), was grown alongside the others and retained the varietal form. It was not analysed statistically. The characteristics of this population have a genetic basis.

The large differences in lemma-length in this species are interesting when considering *G. fluitans* var. *islandica* Löve (1951), largely because of its short lemmas (mean 5.9 mm., range 5.3-6.4 mm.). The British material studied by Löve had a range of 6.3-7.6 mm. Fig. 2, however, shows that races K and O have short lemmas very similar in range to var. *islandica* (5.4-6.4 mm., mean 5.86 mm., in race K; and 5.2-6.2, mean 5.73 mm., in race O). This variety is therefore to a large extent paralleled by British material.

Glyceria fluitans has a greater range of variation in race means for spikelet and leaf homotypes than the other species (Fig. 1). This is shown for leaf index in Fig. 3, and for spikelet characters of *G. declinata* and *G. fluitans* in Table 4. The existence of a greater range of race-means in *G. fluitans* could be due to greater variability or to accidents

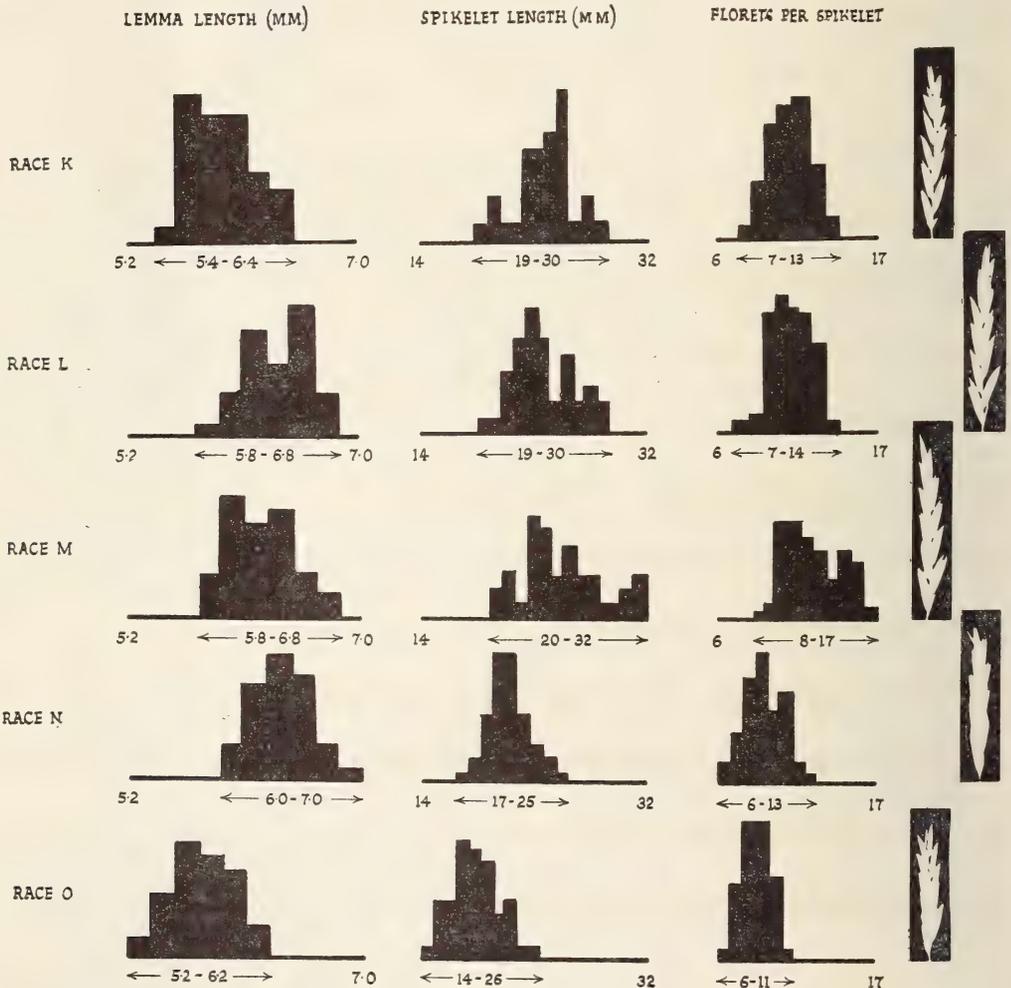


Fig. 2. Spikelet characteristics in five races of *Glyceria fluitans*. The three characters illustrated show a wide range of variation. Spikelet length and number of florets per spikelet are closely correlated. Lemma length varies independently.

of sampling, since it is possible that another five populations could show a smaller range of variation. The intrinsic variability therefore was studied.

The standard deviation is generally used to measure variation and this is expressed as a percentage of the mean, and the resulting coefficient used as an index of phenotypic variation. For this to be reliable, an increase in the mean must be accompanied by a proportional increase in the standard deviation. Day & Fisher (1937) pointed out that there is no logical reason for this, and evolved the more complex analysis of covariance which has been used in population studies by Gregor & Lang (1950), and Baker (1953).

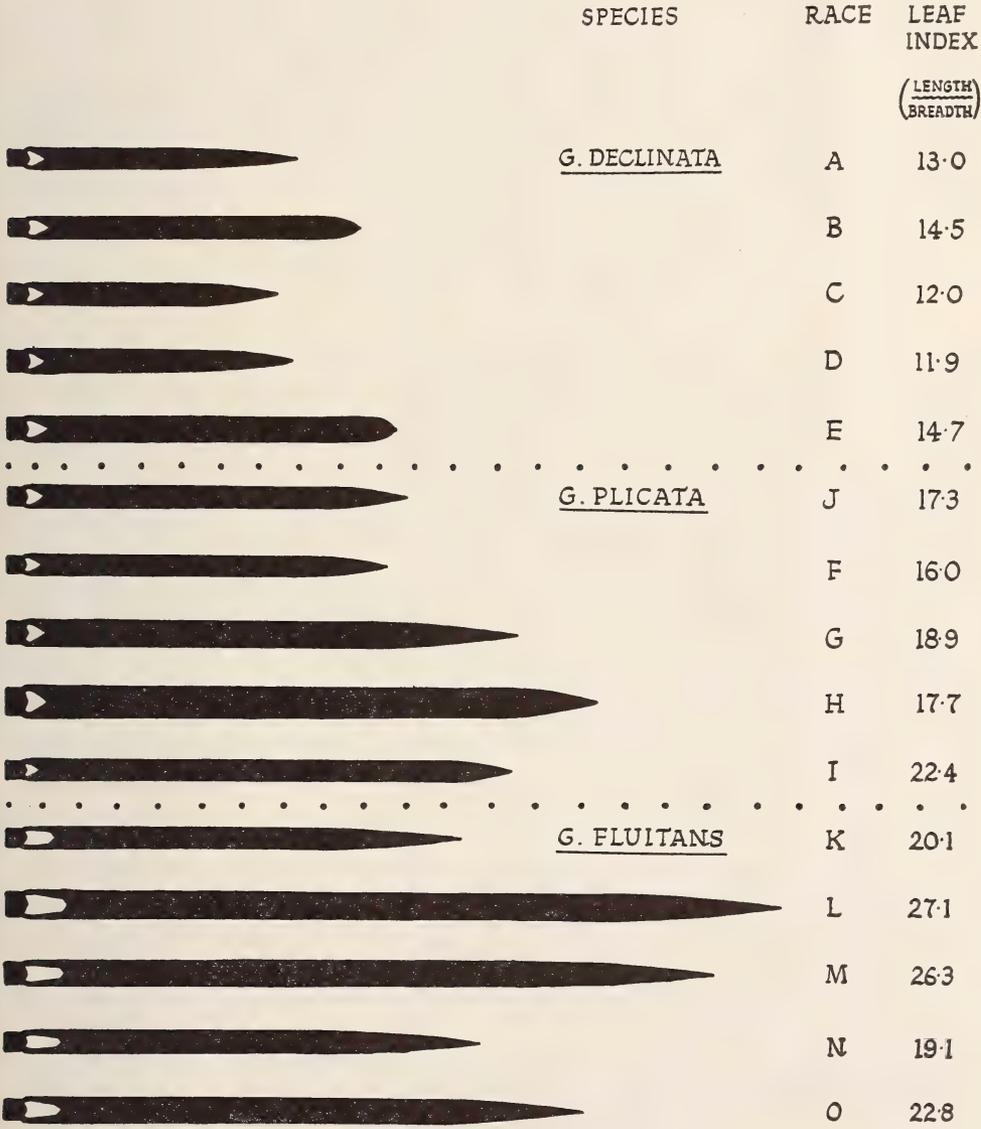


Fig. 3. Leaf morphology.

Variation in leaf morphology in *Glyceria* species. Differences significant at $P = 0.01$ occur between BE : CD : A, FJH : G : I, KN : LM : O, in leaf index, which is a measure of leaf shape. *G. declinata* has the least range of variation, 2.8 units, *G. plicata* a greater range, 6.4 units, and *G. fluitans* the largest range, 8.0 units.

TABLE 4. Range of subpopulation means in *Glyceria* species.

Characters	<i>G. declinata</i>					Range	<i>G. fluitans</i>					Range
	Race						Race					
	A	B	C	D	E		K	L	M	N	O	
Lemma length	4.73	4.87	4.58	4.84	4.72	0.29	5.86	6.39	6.24	6.42	5.73	0.69
Spikelet length	15.00	16.36	14.32	15.22	15.43	1.36	24.50	25.90	25.40	20.80	18.00	7.90
No. of florets per spikelet	6.27	7.87	7.09	7.37	7.73	1.60	10.10	11.20	12.42	9.16	8.48	3.94

The standard deviations of the races of *Glyceria* were therefore plotted against the means in order to see whether they were related. Fig. 4 illustrates the results for spikelet-length in *G. fluitans* and *G. declinata*; for lemma-length in *G. fluitans*, and for the species as a whole, based on the pooled data of the races.

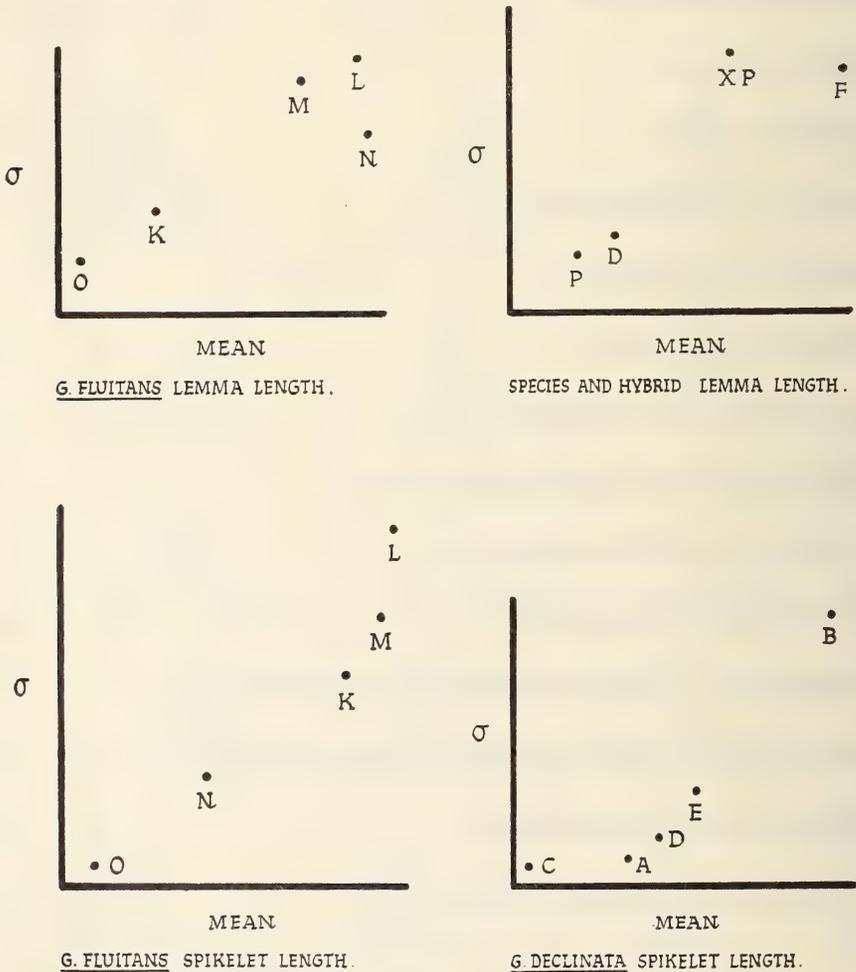


Fig. 4. Relation between mean and standard deviation in *G. fluitans* and *G. declinata*. Race letters : *G. fluitans* K L M N O ; *G. declinata* A B C D E . Symbols for species : D = *G. declinata* ; P = *G. plicata* ; F = *G. fluitans* ; XP = *G. x pedicellata*.

TABLE 5.
Coefficients of variation in *Glyceria*.

Character	Species	Details of data	Population ¹ mean (mm.)	Standard deviation (σ)	(per cent) Coefficient of variation
Lemma length	<i>G. plicata</i>	Pooled	4.45	0.175	4.06
		Most variable Race J	4.51	0.189	4.18
" "	<i>G. declinata</i>	Pooled	4.73	0.200	4.22
		Most variable Race D	4.84	0.232	4.79
" "	<i>G. fluitans</i>	Pooled	6.21	0.402	6.48
		Least variable Race O	5.73	0.345	6.07
" "	<i>G. × pedicellata</i> ²	Pooled	5.47	0.434	8.11
		<i>G. declinata</i>	Pooled	15.26	0.872
Spikelet length	<i>G. declinata</i>	Most variable Race B	16.36	1.166	7.12
		Pooled	22.89	3.967	17.31
" "	<i>G. fluitans</i>	Pooled	18.00	2.491	13.83
		Least variable Race O	18.00	2.491	13.83

1. All differences between species significant at $P = 0.01$

2. Data from specimens in Herb. University of Leicester.

The coefficients of variation for lemma-length, given in Table 5, based on the pooled data, show that *G. fluitans* is the most variable species; and this is confirmed by the fact that the coefficient of variation for the least variable race of *G. fluitans* exceeds the coefficient of variation for the most variable races of the other species.

The vegetatively propagated hybrid, *G. × pedicellata*, has a similar ecological distribution to the sexually-reproduced species, but a very different genetic population-structure, and it is therefore impossible to carry out sampling on a comparable basis. Data for lemma-length were therefore collected from a random selection of herbarium specimens. The results are shown for comparison in Table 5. *G. × pedicellata* has a smaller mean-lemma-length than *G. fluitans* but a larger standard deviation and therefore the highest coefficient of variation. In the first paper of this series (Borrill 1956a), it was concluded that *G. × pedicellata* had a greater range of phenotypic variation than either parent in panicle characters; the present data suggest that it might also have a higher variability.

CONCLUSIONS

1. The small, spatially isolated, local populations sampled have many statistically significant phenotypic differences which show that underlying genetic differences exist.
2. In one population of *G. fluitans* var. *triticea*, the varietal type of morphology was found to have a genetic basis.
3. *G. fluitans* var. *islandica* Löve is similar to two British populations of *G. fluitans* with short lemmas.
4. The phenotypic characters fall into three correlation groups: those concerned with the dimensions of the vegetative parts, those providing a measure of plant bulk, and the spikelet characters. *Lemma-length* was independent.
5. *G. fluitans* is more variable than *G. declinata* and *G. plicata*.
6. In an earlier paper (Borrill 1956a), *G. × pedicellata* was shown to have a greater range of variation than either parental species; the present data suggest that it may have a greater variability. The evidence obtained is not conclusive, because population-sampling could not be put on the same basis in parents and hybrid.

7. All the populations of *G. declinata* and *G. fluitans* studied headed in the first season, whereas, in *G. plicata*, two of the populations headed in the first season, two remained non-heading, and one was intermediate. All the seed- and population-plants were without low temperature treatment.

8. There was no obvious relation between the nature and extent of morphological differentiation in the populations examined and the type of habitat in which they grew. The implications of this will be discussed in a further paper.

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A BIOSYSTEMATIC STUDY OF SOME *GLYCERIA* SPECIES IN BRITAIN*

4. BREEDING SYSTEMS, FERTILITY RELATIONSHIPS AND GENERAL DISCUSSION

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INTRODUCTION

In a previous paper of this series (Borrill, 1958) it was shown that in each of the species, *G. declinata* ($2n = 20$), *G. plicata* ($2n = 40$) and *G. fluitans* ($2n = 40$) of section *Glyceria*, morphologically distinct local populations occur in paludal habitats. Five such populations were studied from each species, and shown to be genetically distinct. The results of a study of the breeding systems and fertility relationships of some of these populations (cf. Borrill, 1955) are given in the present paper, followed by a general discussion of the series of four papers.

MATERIAL

The populations were sampled by collecting two seed heads from each of between 10 and 12 plants spread over the area of the population. The limits of individual plants were explored in an attempt to ensure that seed was not derived from a single clone. The seed was pooled, and 24 plants, raised from a bulk lot of this seed, were used as a sample of the potential biotypes present in the population.

The population samples used, to be called "races", are shown in Table 1, attention being concentrated on those of the tetraploid species *G. plicata* and *G. fluitans*. The morphology and habitats of the seed parents were described fully in the third paper of this series (Borrill, 1958).

TABLE 1.

Races used in fertility studies.

Species	Race	Origin of seed parents			
		Locality	Vice-County		
<i>G. declinata</i>	A	Malham Beck	Mid-West York	64	
	C	Ulverscroft	Leicester	55	
	D	Cadgwith	W. Cornwall	1	
	E	Hopedale	Stafford	39	
<i>G. plicata</i>	F	Fulbourn	Cambridge	29	
	G	Breedon	Leicester	55	
	J	Wittering	Northampton	64	
<i>G. fluitans</i>	K	Breedon	Leicester	55	
	L	Ulverscroft	Leicester	55	
	N	Acle	E. Norfolk	27	
	O	Acle		E. Norfolk	27
				E. Norfolk	27

* 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 of Leicester.

METHODS

The methods of making crosses were based on those described by Jenkin (1924, 1931). The florets to form the female unit were emasculated by hand and enclosed with inflorescences of the pollen parent in glassine paper bags. To study self-fertility, groups of heads were enclosed in pollen-proof bags. These operations were carried out on dry, calm days. The smallness of the florets and anthers made it impossible to emasculate by extracting the anthers with forceps. Anthesis occurs immediately the spikelets have emerged; therefore, as soon as this occurred, the leaf sheaths were split down and the divided portions tied back. Spikelets which had flowered, and those which were too soft to manipulate, were removed. The inflorescence was fastened to a sheet of glass, using plasticine strips, and emasculation was carried out with mounted needles under a low-powered binocular microscope. Any burst anthers and stray pollen were easily seen, and the florets containing them were discarded. After emasculation the leaf sheaths were tied back lightly into place round the culm thus providing mechanical support and reducing the risk of the florets drying out.

After the spikelets shattered on the ripe culms, the bags were opened and the seed spread on a ground-glass plate lit from below. The seed from the bag was divided into two classes, heavy seed, which was judged to be fully developed, and light seed, this category including all seed which, though rounded, was nevertheless below two-thirds of the normal size, also seed which was shrunken and imperfect. A sample of ripe seed collected in the field was used as a standard for the comparison of seed size.

In the emasculated inflorescences, a definite number of florets was used, and the percentage seed set calculated directly. In the selfed- and open-pollinated panicles the total number of florets used was found by counting the number of persistent glume-pairs, which gave the number of spikelets present, and multiplying this number by the mean number of florets per spikelet for the race, obtained from the biometrical data given in paper 3 (Borrill, 1958). A correction factor of 1.5 florets per spikelet was deducted to allow for the proportion of male-sterile apical florets, which often set no viable seed. Rudimentary terminal florets were ignored.

Self- and cross-compatibility were assessed by the number of seeds set, expressed as a percentage of the maximum possible. The seed was sown on a germinator at 25°C. in order to determine its viability.

BREEDING SYSTEMS

Self-fertility

Seed was collected from open-pollinated heads of *G. plicata* and *G. fluitans* to find the capacity for setting seed when no deliberate restriction was placed on the source of pollen available. The viability of this seed was tested and compared with that of seed collected from the original plants in the field. Plants of all three species were selfed, and the results for seed-setting and viability are summarised in Table 2.

In *G. declinata*, selfed seed only was collected from one plant of each race. These plants were highly self-fertile, with a preponderance of heavy seed, and there was little difference between plants in degree of self-fertility. The viability of the seed compared favourably with that of the open-pollinated seed from the original populations.

Seven plants of *G. plicata* were selfed, and each resembled *G. declinata* in being highly self-fertile, their seed-set being as good as that obtained from open pollination. These races have now been maintained by selfing without apparent loss of vigour through three seasons. The behaviour of *G. fluitans* was entirely different, self-fertility being much lower than cross-fertility. The detailed results (Table 3), summarised in Table 2,

TABLE 2.

Summary of seed setting and viability. (For details of *G. fluitans* see Tables 3 and 5).

Method	Race	No. of selfings crosses or open pollinations	Percentage mean seed-set					Percentage mean germination	
			Heavy	Range	Light	Range	Total	Heavy and light seed	Range
<i>Glyceria declinata</i> Selfings	A	1	62		8			95	
	C	1	67		11			100	
	D	1	64		15			97	
	E	1	83		9			89	
			69*	62-83	11	8-15	80	95	89-100
Open pollination Experimental garden	—	—	—	—	—	—	—	—	—
	Original populations	—	—	—	—	—	—	76	41-93
<i>Glyceria plicata</i> Selfings	F	3	77		6.6			93	
	G	2	90		7.0			86	
	J	2	78		4.5			98	
			81	69-97	6	4-9	87	92	82-100
Open pollination Experimental garden	G	1	81		6			97	
	J	2	85		4			81	
Original populations	—	10	84	81-86	4	2-6	88	83	65-97
								78	57-95
Intra-race crosses	F	5	77		12.8			93	
	J	5	75		10.4			96	
			76	68-81	12	7-17	88	95	90-100
Inter-race crosses	F × J	6	74		8.8			87	
	F × G	1	79		9.0			84	
	J × G	2	76		10.0			87	
			75	70-81	9	6-12	84	86	80-95
<i>Glyceria fluitans</i> Selfings	K	4	27		43			55	
	L	3	19		52			51	
	N	2	28		49			39	
	O	2	37		38			67	
				27	8-58	46	13-67	73	54
Open pollination Experimental garden	K	3	68		22			88	
	O	2	67		13			87	
Original populations	—	12	67	65-71	19	6-23	86	88	87-90
								82	63-95
Intra-race crosses	K	4	60		16			42	
	N	3	59		14			54	
	O	2	71		17			52	
			62	51-75	16	12-19	78	54	30-58
Inter-race crosses	L × N	2	0		0			0	
	L × K	5	2.2		2.4			4.2	
	L × O	3	3.2		7.3			2.6	
	K × N	2	1.0		2.1			0	
	K × O	2	0		0.7			0	
	N × O	3	0		1.8			0	
			1.2	0-11	2.5	0-22	3.7	1.7	0-21

*Figures in heavy type are mean and range percentages.

show that the percentage of heavy seeds is much less on selfing than from open pollination. It is also clear that there is a variation in degree of self-compatibility; for instance, self-fertility is low in plants *K* 1 and *L* 22 (Table 3), and higher in plants *K* 21 and *O* 218. Table 2 shows clearly that, whilst in *G. declinata* and *G. plicata* self-fertility is uniformly

high, it varies widely in *G. fluitans*. The seed-viability data parallel these results since, in general, the most self-fertile plants, with the largest amount of heavy seed, have the highest germination.

TABLE 3.
G. fluitans Seed set and viability from selfing and open pollination.

Method	Race	Plant No.	No. of spikelets	No. of seeds		Per cent		
						Seed set		Germination
				Heavy	Light	Heavy	Light	Heavy plus light seeds
Selfings	K	1	36	27	187	8	57	17
		19	69	126	270	19	41	66
		20	101	308	475	32	49	57
		21	26	126	52	50	25	82
Open pollination	K	1	70	455	156	68	23	90
		8	98	671	198	71	21	87
		13	48	301	104	65	22	No data
Selfings	L	22	62	60	431	10	65	38
		23	73	158	435	22	55	54
		24	9	24	33	25	37	61
	N	3	35	127	9	41	32	76
19		26	36	154	16	67	2	
Open pollination	O	1	51	68	259	16	63	44
		18	13	60	13	58	13	90
	13	107	572	184	68	21	88	
	23	97	514	50	67	6	87	
Totals:								
Selfed			501	1120	2408	—	—	—
Open pollinated			430	2513	692			
Mean per cent:								
Selfed			—	—	—	27.0	45.8	53.6
Open pollinated			—	—	—	67.8	18.6	88.0

Anthesis

The process of anthesis was observed on several occasions, in the greenhouse and out of doors. Anthesis occurs during the morning at a time apparently determined by weather conditions. The terminal spikelets are the first to mature, and maturation then proceeds basipetally node by node. The basal spikelets on each pedicel mature slightly before those above (Plate 8), but anthesis often occurs simultaneously in two or three spikelets on the same pedicel. Within each spikelet, the florets mature strictly from base to apex.

In *G. declinata* (Plate 8), the first sign of anthesis is the slight separation of palea and lemma on a basal floret, followed by the opening of up to six florets in the same spikelet. This process occurs more or less simultaneously in other spikelets. The lemma and palea diverge widely; at the same time the filaments elongate and the rather short, feathery stigmas protrude very slightly. The anthers are small, about 1 mm., standing in the florets at the end of the stiff filaments which equal, or somewhat exceed the length of the lemma. Dehiscence is by two longitudinal slits, many grains being scattered simultaneously, the rest by shaking; the dehisced anthers curl up and shorten appreciably.

PLATE 8.



G. declinata



G. plicata



G. fluitans

Anthesis in *GLYCERIA* species.

Information about spikelet a in text.



The stigmas are apparently fully receptive when the grains are shed. Whether pollinated or not, the florets remain open for up to ten minutes. In *G. plicata* (Plate 8) the course of anthesis is very similar; the stigmas are a little longer and protude slightly from the angle between palea and lemma. The filaments somewhat exceed the lemma. The anthers are up to 1.25 mm. long and contain larger pollen-grains. After the florets have closed, the shrivelled anthers persist for several days.

In *G. fluitans* (Plate 8) up to 4 florets opened more or less simultaneously in any one spikelet*, and the palea and lemma diverge moderately. Immediately on opening, the filaments elongate rapidly, carrying out the anthers, which are over 2 mm. long. The filaments about equal the lemma, being from 5 to 7 mm. long, and become entirely pendulous, the anthers hanging down below the florets. When the anthers are partly exerted, the stigmas begin to expand; these are long and bushy, protruding conspicuously through the angle between the divergent palea and lemma. Repeated observations led to the conclusion that this species is weakly protandrous. This can be illustrated by successive florets of the marked spikelet in Plate 8. In the uppermost floret the three anthers are emerging and one has dehisced and the stigma protrudes but is not yet expanded. In the floret below, the dehisced anthers hang right down and the stigmas are fully expanded. The florets stayed open for up to 30 minutes, and, when they closed, the stigma and filaments were trapped between lemma and palea.

Discussion

It is clear from these results, that *G. fluitans* differs from the other two species in degree of self-compatibility, and in behaviour at anthesis. To assess the breeding system in natural populations, the chances of self- as against cross-pollination must be estimated. Since a plant's own pollen is more readily available than pollen from adjacent plants, self-fertilisation may occur unless there is a mechanism to prevent it. Because of their high capacity for self-fertilisation, *G. declinata* and *G. plicata* can be regarded as largely inbreeding species, and should be added to the rather small group of inbreeding perennial grasses listed by Beddows (1931).

The possibility that apomixis may occur must not be overlooked, but the stimulus of pollination is necessary for seed to be set, because, when four plants were emasculated and bagged to exclude pollen, no seed was obtained.

G. fluitans can be regarded as mainly an outbreeding species because the plants are largely self-incompatible. Self-fertilisation is nevertheless likely to occur up to the full extent of self-compatibility, as in *Lolium perenne*, in which Griffiths (1950) showed that, on average, about 10 per cent of selfing occurred.

It is interesting that, although the breeding system in grasses is primarily decided by the degree of self-compatibility, it is nevertheless associated with differences in floret morphology and behaviour at anthesis. Inbreeding grasses, which are often annuals, tend to have small anthers which are not well-exserted, whereas outbreeding grasses have large, pendulous anthers, with a lot of pollen and some degree of protandry, or, more rarely, protogyny (Beddows, 1931).

In the third paper of this series (Borrill, 1958) it was shown that *G. fluitans* was more variable than *G. declinata* or *G. plicata*. The present results suggest that this is associated with the breeding systems, the outbreeding species, *G. fluitans*, being the most variable.

In circumstances where adaptability, and consequently high variability, is at a selective premium, self-incompatibility has an obvious advantage. Large anthers may have the advantage of distributing the pollen more efficiently, though the total amount of pollen

* According to Arber (1934) anthesis occurs in each spikelet as it emerges from the leaf sheath. The author's observations are that in all three species anthesis often, but not always, occurs in the basal florets of a spikelet just after emergence, depending on the weather conditions.

per plant may be no more than that produced by a plant with small anthers. Protandry, which often exerts no effective control over the breeding system, may merely be a mechanical consequence of rapid elongation in the long filaments associated with the exertion of large pendulous anthers.

FERTILITY RELATIONSHIPS

Interspecific crosses

Six crosses between diploid and tetraploid species were made, and four crosses between tetraploid and tetraploid, using large plants dug up from the field. Crosses between species were attempted in both directions, but reciprocal crosses between the same individuals were not practicable. The data are shown in Table 4. Crosses of diploid and tetraploid were completely unsuccessful, as no trace of seed development was found.

When the seed from the tetraploid crosses was sown on filter-paper pads on a constant temperature germinator, no seedlings were obtained and all the seeds were subsequently dissected. From three crosses of *G. fluitans* and *G. plicata*, 15 light seeds were obtained (11 per cent seed-set). In one seed (cross No. 7), containing an imperfect embryo and some endosperm, the radicle began to grow. Two seeds of cross No. 8 produced a weak radicle and hypocotyl. The other seeds contained the remains of endosperm, or only watery fluid. From one cross of *G. plicata* and *G. fluitans*, 25 seeds were obtained (58 per cent seed-set); these were of approximately normal length, but all were empty except two which contained traces of what was probably endosperm, and none germinated.

TABLE 4.
Interspecific crosses in Glyceria species.

No.	Crosses		No. of florets emasculated	No. of caryopses	
				Heavy	Light
1	<i>G. declinata</i> ♀ (2n = 20) H.446*	×	<i>G. fluitans</i> ♂ (2n = 40) H.440	37	—
	<i>G. fluitans</i> ♀ (2n = 40)	×	<i>G. declinata</i> ♂ (2n = 20)		
2	H.439		H.413	51	—
3	H.435		H.413	62	—
4	<i>G. declinata</i> ♀ (2n = 20) H.413	×	<i>G. plicata</i> ♂ (2n = 40) H.423	35	—
	<i>G. plicata</i> ♀ (2n = 40)	×	<i>G. declinata</i> ♂ (2n = 20)		
5	H.423		H.446	71	—
6	H.441		—	60	—
7	<i>G. fluitans</i> ♀ (2n = 40) H.439	×	<i>G. plicata</i> ♂ (2n = 40) —	49	—
	H.439		H.423		
8	H.437		—	23	—
10	<i>G. plicata</i> ♀ (2n = 40) H.442	×	<i>G. fluitans</i> ♂ (2n = 40) H.440	43	—

* Herbarium citations given in the following abbreviated form: H.446 = Specimen No. 54446 in the Herbarium of the University College of Leicester.

In all the crosses, conditions for pollination were reasonably good, and the entirely negative results of crossing diploid and tetraploids may have some value in that, although the flowering times of the species coincide, triploid hybrids do not appear to occur in the field where the parents grow together. Both Hubbard (1954) and Lambert (1949) found plants which were considered on morphological grounds to be hybrids between *G. fluitans* and *G. declinata*, but the crucial test of the existence of such hybrids is the demonstration of their triploidy. All the doubtful sterile plants found in the present study, whether growing with their supposed parents or not, were examined cytologically and as all had $2n = 40$ they must be regarded as specimens of *G. × pedicellata*.

The result of crossing the tetraploids differs according to the direction of the cross, since, with the outbreeding species *G. fluitans* as pollen parent, a good percentage of normal-sized but empty seeds was obtained. With the inbreeding species *G. plicata* as pollen parent, a smaller number of shrunken seeds was obtained of which three were partially viable. A similar result was obtained by Jenkin (1954a) in crosses between species of *Lolium*, differing in breeding system, where the general picture suggested that "in the self-pollinating annual species the maternal tissues of the ovaries respond readily to pollination by wind-pollinating types, so that the Caryopsis integuments reach full development, even though their contents may be very meagre when the seed is mature. The response of the maternal tissues of the ovaries of *Lolium perenne* to the pollen of the self-pollinating species also follows a general pattern. In this case these tissues do not give a full response and develop only *pari passu* with the embryo and/or endosperm."

The hybrid between *G. fluitans* and *G. plicata*, *G. × pedicellata*, occurs abundantly in nature. The result of crossing these species suggests that the hybrid is not easy to produce, and that the chance of success is greater with the inbreeding species, *G. plicata*, as the pollen parent.

INTRASPECIFIC CROSSES

Inter- and intra-race crosses were made in *G. plicata* and *G. fluitans*, and, because a wide variation in degree of cross-compatibility occurs, especially in outbreeding species, according to the genotype used and the environmental conditions (Jenkin, 1931, Nilsson 1934), the same plants of *G. fluitans* were used in both types of cross, which were carried out as far as possible on the same day.

In *G. plicata*, a number of reciprocal and direct crosses were made within and between races. The results, which are summarised in Table 2, show that the plants were highly cross-compatible both within and between populations, since in both cases the percentage seed-set was as good as that on open-pollinated inflorescences. The seed viability was also very high.

In *G. fluitans* one reciprocal and two direct crosses were carried out within Race K, three crosses within Race N, and two within Race O. The results are summarised in Table 2, from which it appears that the seed-set approaches that in open-pollinated inflorescences, the bulk of the seed being heavy. The viability, however, was lower than that of seed from open pollination. It is worth noting that the range in viability of seed from these crosses was less than that of seed from selfing.

Four reciprocal and nine direct crosses were made between plants from different races of *G. fluitans*. The results are shown in detail in Table 5 and summarised in Table 2. No seed was obtained in the majority of cases. Heavy seed was produced in two crosses only, $L 17 \times K 21$ and $K 8 \times O 4$. Four seedlings were obtained from nine heavy seeds in the former cross, and one from four heavy seeds in the latter. No light seeds germinated. The four F_1 plants of $L 17 \times K 21$ reached maturity, and were phenotypically intermediate between the parents. Further studies of these plants are in progress.

The results suggest that plants within each race of *G. fluitans* were cross-compatible, whereas plants from different races were largely incompatible. In this respect the behaviour of *G. fluitans* is entirely different from that of *G. plicata*.

TABLE 5.
G. fluitans seed setting and viability in inter-race crosses.

Race	Cross: Plant Nos.	Emasculated florets	No. of seeds set		Percentage seed-set		No. of seeds sown	Germination		Empty* seeds
			Heavy	Light	Heavy	Light		Number	Per cent	
L × N	17 × 12	37	0	0	—	—	—	—	—	—
	21 × 16	42	0	0	—	—	—	—	—	—
L × K	17 × 21	84	9	10	10.7	11.9	19	4	21.1	13 + 2†
	18 × 22	26	0	0	—	—	—	—	—	—
	22 × 18	31	0	0	—	—	—	—	—	—
	19 × 23	29	0	0	—	—	—	—	—	—
	20 × 24	35	0	0	—	—	—	—	—	—
L × O	8 × 4	41	4	9	9.75	21.9	13	1	7.69	12
	4 × 8	45	0	0	—	—	—	—	—	—
	5 × 1	40	0	0	—	—	—	—	—	—
K × N	9 × 4	46	0	2	—	4.34	2	—	—	2
	4 × 9	39	0	0	—	—	—	—	—	—
K × O	13 × 8	64	0	1	—	1.56	1	—	—	1
	8 × 13	29	0	0	—	—	—	—	—	—
N × O	20 × 24	54	0	2	—	3.70	2	—	—	2
	19 × 23	25	0	0	—	—	—	—	—	—
	22 × 18	42	0	0	—	—	—	—	—	—
Total		709	13	24	—	—	37	5	—	32
Mean percentage		—	—	—	1.20	2.55	—	—	1.69	—

* Apparently normal seeds, but contained watery fluid only.

† Two seeds with some endosperm present, no embryo.

In assessing the information obtained about fertility relationships, it is clear that, although only a limited number of selfings and crosses were carried out, the results are consistent, which suggests that, from the behaviour of the sample of plants studied, legitimate inferences can be drawn concerning the behaviour of the populations as a whole.

CONCLUSIONS

1. The results of selfing plants of *G. declinata*, *G. plicata* and *G. fluitans* showed that the first two species were highly self-fertile, while the plants of *G. fluitans* were to various extents self-sterile. From this it appears that *G. declinata* and *G. plicata* are generally inbreeding, and *G. fluitans* generally outbreeding. Associated with this, characteristic differences were observed in behaviour at anthesis, and it has been shown that *G. fluitans* has the greatest variability (Borrill, 1958).

2. Attempts were made to cross *G. declinata* (diploid) with the tetraploids, and to cross the tetraploids. Crosses were tried in both directions. No trace of seed development was observed in diploid-tetraploid crosses. In crosses between the tetraploids, although no seedling plants were obtained, seed development differed according to the direction of the cross, and the chance of success seemed greater with *G. plicata*, the inbreeding species, as pollen parent.

3. Inter- and intra-race crosses were made in *G. plicata* and *G. fluitans*. In the first species, all the plants used were highly cross-compatible both within and between races; whilst in *G. fluitans* although plants within a race were compatible, those from different races were generally cross-incompatible.

GENERAL DISCUSSION

The object of this discussion is to consider briefly the evolutionary relationships of the British species of *Glyceria* and the microevolution of local populations, in the light of the information presented in this series of papers.

The three sympatric species, *G. declinata* ($2n = 20$), *G. plicata* ($2n = 40$) and *G. fluitans* ($2n = 40$), appear to be genetically isolated, because gene exchange does not occur between the diploid and the tetraploids, or between the tetraploids, since their hybrid *G. × pedicellata* is completely sterile. They are therefore coenospecies in the sense of Clausen (1951).

Although the affinities of these species have not been fully established, some evidence has been obtained. Cytological analysis reveals some affinity between at least one genome of *G. plicata* and *G. fluitans*, and it is probable that the species have a common ancestor, which may be *G. declinata*. Several lines of study suggest that *G. declinata* and *G. plicata* are closely related, a conclusion different from that reached by Lambert (1949). These are,

1. The species are morphologically very similar and have the same breeding system; as Stebbins (1950) has pointed out, tetraploid grasses generally have the same breeding system as closely related diploids.

2. The occurrence of some quadrivalents in *G. plicata* together with other evidence, suggests that this species may be an autopolyploid based on *G. declinata*. There are, however, some morphological differences between the species, for instance in stolon formation, the genes for which may have arisen by mutation after the formation of the tetraploid species, or may have been contributed by another, as yet unknown, diploid parent.

3. *G. declinata* and *G. plicata* have a similar geographical distribution in Europe*, whereas *G. fluitans* is an outbreeding species widely distributed in north temperate regions.

The species of section *Glyceria* occur in Britain as small local populations in paludal habitats. When some of these were studied experimentally, it was found that their distinctive morphological features were genetically determined; they nevertheless appeared to have no ecologically adaptive significance. The situation can be contrasted with that demonstrated by Gregor (1944) in *Plantago maritima* populations inhabiting a range of habitats in coastal mud flats, and having a discontinuous distribution. These local populations could be arranged in ecoclines, and merited the status of ecotypes – “the product arising as a result of the genotypic response of a species to a particular type of habitat” (Turesson 1922).

* *G. declinata* is apparently introduced in California and Nevada according to Church (1949).

The *Glyceria* populations studied are not ecotypes, but this does not mean that ecotypes do not occur in the group, since there is at least one in *G. fluitans*, a form with a rather stiff type of leaf, and a simple spiciform inflorescence, which is apparently the result of the parallel response of different biotypes to acid habitats. In the other species the occurrence of ecotypes is less certain. Lack of adaptive significance in the phenotypic differentiation of *Glyceria* populations suggests that the selection pressure is not very effective on the features studied; this may be in part due to the fact that paludal habitats have a certain uniformity. The basic requirement for survival appears to be that the species should be physiologically well adapted to seedling establishment and subsequent growth in wet soil. This means that they have a competitive advantage as colonisers of paludal places, which are often disturbed or open habitats, considerable morphological variation occurring independently of this physiological adaptation.

An examination of the genetic structure of the population may help in understanding how morphological differences have arisen. The variability of inbreeding species is small, compared with that of outbreeders, which carry a large reserve of variability in the heterozygous state. This has been shown experimentally by Gregor & Lang (1950) in *Plantago*, by Baker (1953) in *Armeria*, by Cooper (1954) in *Lolium*, as well as in *Glyceria* (Borrill, 1958). Breeding systems in nature are not mutually exclusive, however. For instance, Griffiths (1950), using genetic markers, showed that, in the generally outbreeding species, *Lolium perenne*, on an average, about 10 per cent self-fertilisation could occur. Similarly in inbreeders some outcrossing may occur, up to 1 per cent, for instance, in self-fertilising cereals (Hays & Immer, 1942).

What is the effect of small population size on species differing in variability to the extent that *G. declinata* and *G. plicata* differ from *G. fluitans*? In inbreeders each population founded by one or more individuals is likely to differ morphologically from other populations, and, provided these are not contiguous, self-fertilisation *per se* will eliminate introgression and therefore reproductive isolation will be complete. This is probably the main reason why in these inbreeding species we find that distinct sub-groups, each with little variability, are easily recognised.

In outbreeders, such as *G. fluitans*, small population-size is likely to have a considerable effect independent of the selection pressure, because :

1. Local populations are likely to be morphologically different owing to their origin from small, unrepresentative biotype-samples; for instance, populations may arise from the chance introduction of a few seeds.

2. The small number of individuals will result in a change of genetic environment (Mayr 1954) which may change considerably the selective advantage of genes. Furthermore, there will be an increase in the number of homozygotes which are exposed to selection, and, under these circumstances, genes will be favoured which are especially viable in the homozygous state. Thus, in a small population, the genes which have the greater viability may not be the same as those in the population from which the founder-plants came; they will be selected for, and phenotypic changes will occur, which may be rapid, even though the environment may be similar to that from which the founder-plants originated.

3. The occurrence of genetic drift (Wright, 1931, 1940) resulting in the random fixation of morphological markers.

Genetic mechanisms therefore exist whereby morphological population differentiation, of no apparent ecological value, can take place in *G. fluitans*. The situation in this species is comparable with that in *Iris virginica* (Anderson, 1936), a species which occurs in isolated small colonies in paludal habitats. The morphological characteristics of the populations are unrelated to the type of habitat, and, furthermore, the differences between populations

are not proportional to the distances separating them; as Dobzhansky (1937) has pointed out, this is a good example of the occurrence of genetic drift. It can be surmised that some of these genetic changes, associated with small population size, have operated in *G. fluitans*.

Evidence has been obtained to suggest that there is a reduction in the cross-compatibility of some *G. fluitans* populations. Examples of cross-incompatibility within a species, not associated with differences in chromosome number, have been described in *Elymus glaucus* (Snyder, 1951), in *Lolium perenne* (Jenkin, 1954b), and in *Oryza sativa* (Tereo & Midusima, 1939). In the last species there was a wide range of variation in degree of sterility amongst the F_2 progeny of partially sterile F_1 hybrids, indicating polygenic inheritance of incompatibility factors.

In outbreeding species considerable spatial isolation is required to prevent gene-flow; for instance, in *Lolium perenne*, isolation must exceed 200 yards from the nearest large source of pollen to reduce contamination below 4 per cent (Griffiths 1950). Cross-incompatibility could therefore be an important factor in genetic isolation, but there are certain difficulties in accounting for the origin of incompatibility between populations of *G. fluitans*. Cross-incompatibility must occur at random by mutation or chromosomal re-arrangement, and would spread only if selectively advantageous, that is, if gene exchange between populations reduced their fitness to their habitats. The evidence suggests, however, that the phenotypic differences between populations are not linked to physiological characters of adaptive value, and, if the incompatibility factors are selectively neutral, there is no apparent reason why they should spread in the population. Further work is required on incompatibility between local populations in *G. fluitans*.

Some paludal habitats are quite stable, while others, especially those by moving water, will be unstable. It is probable that small populations of *G. fluitans*, isolated for a short time, may change appreciably, since the rate of microevolution is more rapid in small populations than in large ones (Mayr 1954), whether the differentiation which occurs is adaptive, or is due to changes in genetic background or to drift. The origin of small populations is accompanied by a reduction in variability, and those which, thus depleted, retain the capacity for further change must be highly heterozygous. The outbreeder, *G. fluitans*, should possess this capacity which is probably reflected in the great geographical range of the species.

In this connection, *G. fluitans* var. *islandica* Löve is of interest, because small local populations similar in their short lemmas have been found in Britain. Löve (1951) suggests that the morphological features of the variety "are the result of long isolation of the Icelandic populations, together with strong selection by climatic factors during at least the last glaciation"; but it is also possible that var. *islandica* is entirely derived from the accidental introduction of a few plants with short lemmas, especially in view of the fact that, according to Löve, the varietal characteristics are apparently not linked to any feature of physiologically adaptive value.

The taxonomic status of local populations of *Glyceria* must be considered. They are not ecotypes, and there is as yet insufficient evidence to call those of *G. fluitans* ecospecies; in any case the tendency to emphasise incompatibility-barriers assessed experimentally has certain disadvantages, since what matters from the standpoint of microevolution is the occurrence of reproductive isolation in nature (Cain, 1953) and, as has been indicated, this may occur in several ways. The Icelandic form of *G. fluitans* has been accorded varietal status by Löve (1951). Many local races of *Glyceria* species in Britain are as distinct as this, and could be given varietal names. However, in my view, it is better, while noting that these forms exist, to await a more extensive study of the group before proposing additional names.

ACKNOWLEDGEMENTS

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SOME TAXONOMIC INVESTIGATIONS ON THE GENUS *RHINANTHUS*

By D. J. HAMBLER

Nigerian College of Arts, Science and Technology, Ibadan

PREFACE

This paper represents part of a thesis accepted for the Degree of Doctor of Philosophy of the University of London. The work was carried out at Queen Mary College with the aid of a maintenance allowance from the Department of Scientific and Industrial Research.

The author's comments and conclusions on *Rhinanthus* are based on study of the specimens in Herb. Mus. Brit.; on field observations at numerous British, and several Swiss localities; on cytological investigations; and on experiments in which *Rhinanthus serotinus* (Schönh.) Oborny (British and Finnish), *R. cf. angustifolius* C. C. Gmel. (Swiss), *R. hirsutus* Gremlé (Swiss), and *R. minor* L. (from a number of British localities, one Swedish and one Swiss locality) were cultivated from seed in England.

The following material is represented in the author's private herbarium:—

65 gatherings from Britain (nos. 1-65), 10 sheets of British and European specimens cultivated in England (nos. 66-75), 2 sheets of Swedish specimens (nos. 76-77), 11 sheets of Swiss specimens (nos. 78-83 and 100-104) and 16 sheets of Canadian specimens (nos. 84-99); of these nos. 1-38 and 78-83 are from populations studied in the field by the author.

The material of the original thesis has been considerably abridged. A fuller account of the investigation may be obtained by reference to the original thesis in the library of the University of London.

INTRODUCTION TO THE LITERATURE

Linnaeus provided the original generic and specific names for *Rhinanthus* in 1753 when he published the name *Rhinanthus crista-galli*. *Rhinanthus* is a critical genus. J. Sterneck, who published his "Monographie der Gattung *Alectorolophus*" in 1901, listed 51 species for which as many as 179 synonyms were given; the number of synonyms for single taxa ranging from 0-15. Other continental workers, notably Chabert, Soó and Poverlein, published taxonomic papers on the genus *Rhinanthus*; references to their works appear in the Bibliography. Druce (1901), Marshall (1903) and later Wilmott (1940, 1942 and 1948) produced papers on the British forms of *Rhinanthus*, Wilmott's 1940 and 1942 papers being the last major taxonomic works published on the genus. Wilmott gave an account of the literature in relation to British *Rhinanthus* in his paper "Some Remarks on British *Rhinanthus*" (1942, 361-379).

THE TWO MAIN TAXA IN BRITAIN

The genus *Rhinanthus*, even within the British Isles, cannot here be studied in its entirety. The field has been limited therefore to one (*R. minor* L.) of the two species which are easily distinguished by their corolla morphology. These species are *R. minor* L. and *R. serotinus* (Schönh.) Oborny, the names replacing the extensively used *R. minor* Ehrh. (non L.) and *R. major* Ehrh. (non L.) respectively, both of which are to be rejected as later homonyms.

Evidence was presented in detail in the original thesis to show that the two taxa could only be separated satisfactorily on corolla characters. Characters such as bract form and colour, and shape and colour of the corolla teeth were found to be variable in both taxa, the degree of variability overlapping; both white and violet teeth, for example, occur in each taxon. Bract shape and tooting have been mentioned by various writers e.g. Wilmott (1942) and Warburg (1952) as diagnostic characters.

Plate 9 illustrates the bracts from specimens of *R. minor* and *R. serotinus* from a Kentish

chalk quarry (at Halling) and a plant grown from seed from Easthaven, Angus (in a London greenhouse), respectively. Considerable similarities are evident. The tothing is equally deep in members of both series, whilst bracts of similar shape occur on each plant.

The corollas of *R. minor* and *R. serotinus* (Fig. 1) may be easily distinguished, the most conspicuous difference being the upcurving of the corolla in *R. serotinus*.

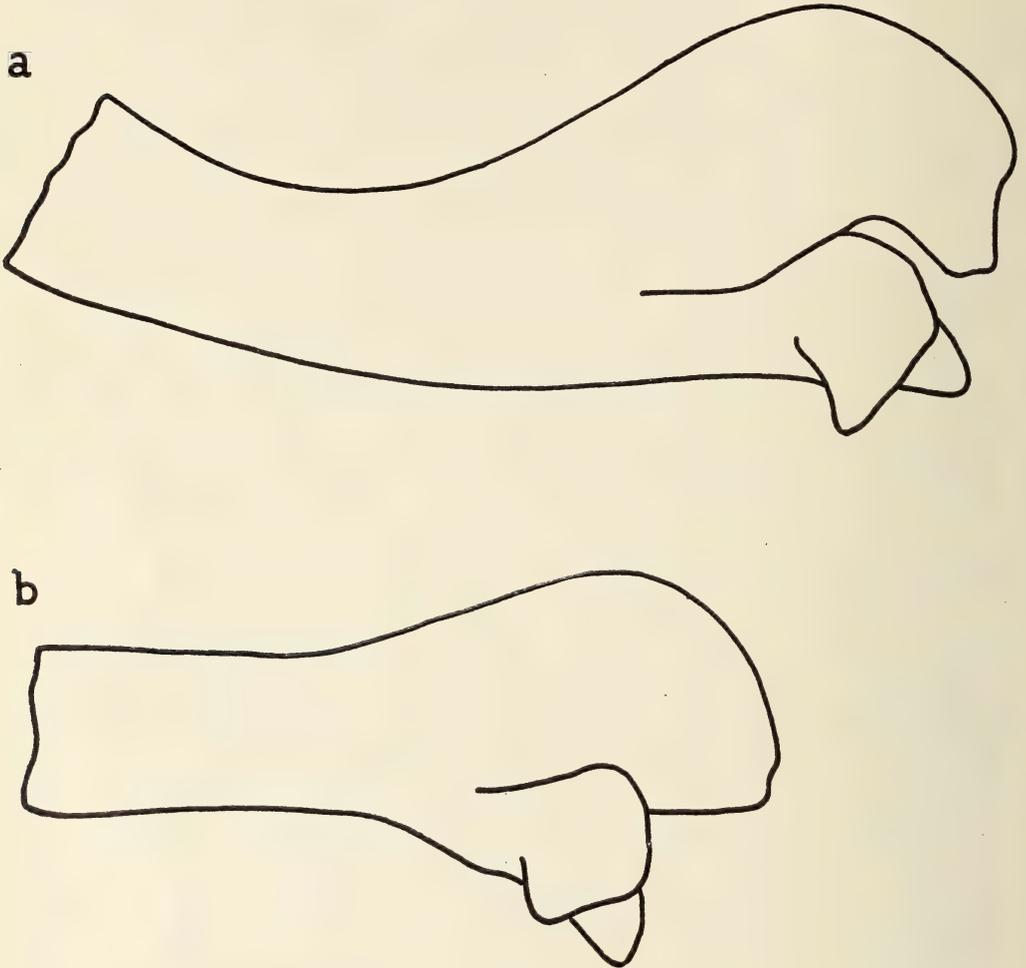


Fig. 1.

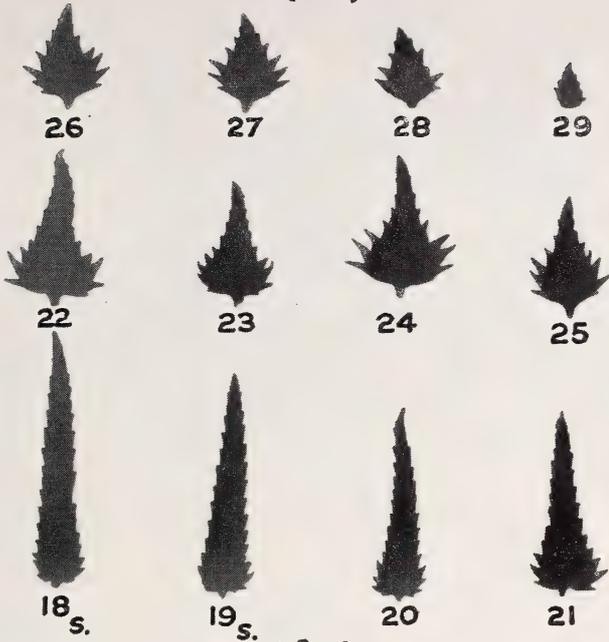
- a = Corolla of *R. serotinus* (Schönh.) Oborny. (Cultivated specimen; seed from Scotland.) $\times 10$
 b = Corolla of *R. minor* L. (From Kent.) $\times 10$

THE PRESENT STATE OF THE TAXONOMY OF RHINANTHUS MINOR L. IN BRITAIN

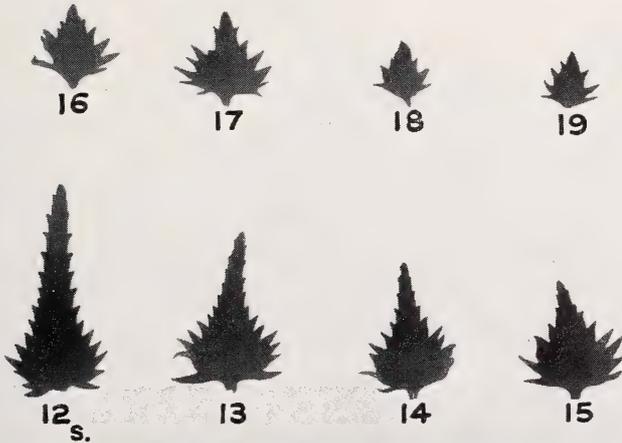
The most recent taxonomic publications on British *Rhinanthus* are those of A. J. Wilmott. The number of British taxa with a straight corolla-tube which he recognised is uncertain, but he appeared to accept the following: *R. minor* Ehrh., *R. minor* var. *robustus* Druce, *R. stenophyllus* (Schur) Druce, *R. borealis* (Sterneck) Druce, *R. spadiceus* Wilmott, *R. spadiceus* subsp. *orcadensis* Wilmott, *R. borealis* var. *calvescens* Wilmott, *R. lintoni* Wilmott, *R. lochabrensis* Wilmott and *R. vachellae* Wilmott, that is a minimum of eight species, all of which are covered by Linnaeus' diagnosis of *R. minor* L. Of the species mentioned above, *R. minor*, *R. stenophyllus* and *R. borealis* are the only ones which do not appear to be endemic. Soó (1929, 185) described various taxa belonging

PLATE 9.

(a)



(b)



(a) Bracts of *R. serotinus* (Schönh.) Oborny.

(b) Bracts of *R. minor* L.

Numbers indicate node numbers from stem base.
s = sterile bract (intercalary leaf).

Vertical line shows length of bract 18s.



to the "Minores" and Wilmott (1942, 367) wrote "Once again, I must admit that I cannot fit the characters given by Soó to the British material I have seen: all sorts of intermediates seem to occur." Wilmott, however, described the existence of forms intermediate between some of the species which he appeared to accept as occurring in Britain. Wilmott's species were described from herbarium material and, even whilst applying new names, he suggested that descriptions might need alteration. Quotations in the following paragraph illustrate some of his doubts.

In his description of *R. spadiceus*, Wilmott stated that he was ". . . not completely satisfied as to the status of this plant. In some localities it is found comparatively uniform and unmistakable, and seems to deserve the rank of species which it has been given"; in his description of *R. vachellae* he remarks ". . . whether it is really a distinct species, must await further material. Meanwhile, however, it needs a name . . ." In his paper in the *Journal of Botany* (1940) Wilmott wrote "The characters given for the new forms here described, being based on a limited number of specimens, also require testing in the field . . .", and "It may be useful to add determinations of, or remarks on, the remaining gatherings in Herb. Mus. Brit. which have been identified as "*Drummond-Hayi*," in one or other nomenclatural combination. Some of them do not agree with *R. borealis*, *R. Lintoni*, and *R. lochabrensis*, and whether the descriptions of these require modification or whether there remain still further forms to be described, must await further investigation." Wilmott mentioned intermediates between *R. stenophyllus* and *R. minor*. He stated (1948, 84) that *R. vachellae* is "somewhat intermediate" between *R. stenophyllus* and *R. spadiceus*, but no indication of the manner in which it is intermediate was given. He stated that *R. borealis* is "somewhat like" except in pubescence of the calyx "the small chalk-down form of *R. minor*", and mentioned a series which "contains some specimens with normally puberulous calyx and one with glabrous calyx (except, of course, on the ciliate margin), and various degrees of glabrescence between the two extremes are shown by the remaining specimens"; Wilmott called the intermediate forms *R. borealis* var. *calvescens*. It might also be noted at this point that Wilmott indicated that *R. vachellae*, a species "with pubescent calyx", "looks extremely like some of the plants collected near Affric Lodge, which had glabrous calyces." The above quotations indicate some of the difficulties which confront the orthodox taxonomist and which made it necessary for Warburg to write in 1952 (*Flora of the British Isles*, 889) "Experimental work on the genus, and on this aggregate (*R. minor* agg.) in particular, is badly needed."

Before beginning an experimental study of a genus, it is useful to assess how far orthodox taxonomy has succeeded in separating morphologically distinct forms. The characters in general taxonomic usage for the genus have been scrutinised, and a check has been made on Wilmott's descriptions and diagnoses of British species by a comparison of these diagnoses with one another, and by reference to the holotype specimens in the herbarium of the British Museum. (It should be noted here that a herbarium sheet labelled "Holotype" exists in Herb. Mus. Brit. for each of the *Rhinanthus* species named by Wilmott. He usually labelled one of the specimens on each sheet as the holotype. Three unlabelled specimens are on the sheet of *R. vachellae*; the best-developed specimen will be regarded here as the holotype.) Some reference to other species recorded for the British Isles has also been made. Various characters used in the taxonomy of *Rhinanthus* will now be considered in turn and an attempt will be made to assess the value of each.

FLORAL MORPHOLOGY WITH PARTICULAR REFERENCE TO THE COROLLA.

The characters of the corolla which have been used in the taxonomy of *Rhinanthus* are length, shape, and features of the corolla teeth. These will be discussed in turn.

The greatest variation in corolla length in the described British forms is small; all fall into the range 13-15 mm. I consider this character to be of extremely doubtful value since I have found it to be affected by environmental influences; for example plants cultivated in the absence of a host plant produced corollas smaller than those typical of plants of similar origin which were attached to hosts.

The descriptions of the British species named by Wilmott were made mostly from dried material (see, for example, Wilmott, 1942, 374). It must therefore be expected that corolla morphology might not have been easily discernible. For example, in the description of *R. spadiceus* subsp. *orcadensis* (Wilmott, 1942, 369), it is stated that "the corolla . . . in the dried plant, seems to be broader and the lower lip looks larger." My own field notes relating to plants with a general similarity in habit to the type specimens of this taxon, and which were collected from heathland on Orkney Mainland, indicate that the corollas of these plants were similar to those of larger specimens of *R. minor* growing elsewhere. The only other description of corolla shape which is given in Wilmott's papers on *Rhinanthus* appears to be a reference to the "large and peculiar-shaped" corolla of *R. lochabrensis* which was mentioned in his paper describing *R. vachellae* (1948, 84). No measurements appear to have been published of the corolla of *R. lochabrensis*, and no qualifying statement seems to have been made.

My own observations of the corollas of living British and Continental specimens support my conclusion that a group of the genus, *R. minor*, is characterised by a more or less uniform corolla morphology and appears to be adapted by the ultimate position of the stigma for self-pollination. The slight variations in the proportions of the lobes of the corolla which may occur are such that they do not lend themselves to written description. It is, in any event, evident that the morphology of the corolla, which might be expected to provide some of the strongest evidence for specific differences, has received little more than casual attention in the diagnosis of British endemic taxa.

The length and shape of the corolla teeth have been used in diagnoses and descriptions of British *Rhinanthus*; it is difficult, however, to consider specimens in relation to diagnoses where no standard is given. For example, the teeth of *R. lochabrensis* are "more projecting than in *R. Lintoni*" (Wilmott, 1940, 212), whilst the teeth of *R. lintoni* are "narrow scarcely projecting" (Wilmott, 1942, 374). In my experience, the variation in the shape of the corolla teeth in *R. minor* appears to be continuous from the condition in which the teeth are so short as to be scarcely recognisable, to that in which they are about 1 mm. in length. There is some evidence that tooth-shape, at least in part, reflects genetic differences, since plants from different localities (when cultivated under similar conditions by the present writer) were found to be distinguishable by their corolla teeth. However, it is evident that written descriptions, such as appear in the diagnoses of the British endemic forms, are inadequate for use in the practical determination of species.

SHAPE AND MEASUREMENTS OF THE CALYX

The shape of the calyx appears to have been regarded as important in the diagnoses of British *Rhinanthus* species by Wilmott, as does the measurement of length and breadth. Descriptions of the shape and measurements of the calyx are published in Wilmott's specific diagnoses, and in the descriptions of species given by Warburg in the *Flora of the British Isles* (1952). I have examined critically the published figures and have compared them with the written descriptions of shape, and, where type material is available in Herb. Mus. Brit., I have compared the published data with my own measurements of this material. My measurements were of the maximum dimensions of the most mature calyx of each holotype specimen (to the nearest 0.5 mm.).

In order to facilitate comparison of the various sets of data, length and breadth measurements may be combined into a simple shape index "S" calculated from the equation:

$$S = \frac{\text{Breadth of calyx}}{\text{Length of calyx}} \times 100$$

Indices derived from measurements published in the literature will henceforth be referred to as " S_L ", whilst indices derived from measurements of the holotype specimens will be referred to as " S_T ". These indices, together with the measurements from which they were derived, are given in Table I below.

Key—*Warburg (1952, 890).

†Wilmott (1942, 373).

TABLE 1.
Measurements and shape indices for the calyces of British *Rhinanthus* "species."

Species	Holotype Length	Specimen Breadth	S_T	Literature		S_L
				Length	Breadth	
<i>R. minor</i> Ehrh.	—	—	—	—	—	—
<i>R. stenophyllus</i> (Schur) Druce				14-16	10-12*	71.43-75.00
<i>R. calcareus</i> Wilmott	11.50	8.50	73.91	c.12	9-11	75.00-91.67
<i>R. spadiceus</i> Wilmott	11.50	10.50	91.30	11	8	72.73
				12	9	75.00
				11	10	90.91
				(14	9½)	(67.86)
subsp. <i>orcadensis</i> Wilmott	8.00	7.50	93.75	—	—	—
<i>R. borealis</i> (Sterneck) Druce				18	17†	94.44
var. <i>calvescens</i> Wilmott	15.50	13.00	83.87	—	—	—
subsp. <i>salmoni</i> Soó	11.00	8.50	77.27	—	—	—
<i>R. lintoni</i> Wilmott	11.00	9.00	81.82	12	9½	89.15
				9½	10	105.26
				13	11	84.62
<i>R. lochabrensis</i> Wilmott	13.00	11.00	84.62	13	11½	88.46
				17	13½	79.41
<i>R. vachellae</i> Wilmott	10.00	8.00	80.00	—	—	—

Measurements from the literature are those given in the original diagnosis of each taxon except where indicated in Key. All measurements are given in mm.

— indicates no measurement available.

Some considerations of written descriptions of shape in relation to shape indices follow :

1. From the table it is evident that all the species listed fall, with regard to S_L , within the range for *R. spadiceus*, i.e. between 67.86 and 90.91. The S_L of 105.26 calculated for *R. lintoni* is probably a result of a misprint (see 4 below) and has been ignored here, whilst I consider the S_L of 91.67 calculated for *R. calcareus* to be negligibly in excess of the highest figure for *R. spadiceus*. From these considerations it appears that the description of shape of the mature calyx which is given in the diagnosis of *R. spadiceus* should cover all the other species here listed. Since all the descriptions in the literature cited are worded differently it is difficult to judge whether this is in fact the case.

2. The description of *R. lochabrensis* (Wilmott, 1940, 212) indicates that the calyx is at all times "considerably longer than broad"; the maximum S_L for this species is 88.46.

The minimum S_L calculated for *R. lintoni* is 84.62, and the description for this species runs "nearly as broad as long" (Wilmott 1940, 210). From these examples, it would appear that the written descriptions are at variance with the published measurements, since if a calyx whose breadth measurement is c. 89% of its length is "considerably longer than broad", one with a corresponding percentage of c. 85 can hardly be described as "nearly as broad as long". It is also relevant to note that at least one of the specimens on the holotype sheet of *R. lochabrensis* has $S_T = 100$, i.e. an almost round calyx. The description of the calyx of *R. lochabrensis* would therefore appear to be inaccurate, although the italics used by the author indicated that he attached considerable importance to it.

3. The description of the calyx of *R. calcareus* appears to be at variance with the published measurements. The smallest value for S_L in this case is 75.00 which is 4.41 less than the smallest value for *R. lochabrensis* whose calyx is "considerably longer than broad"; the description of the calyx as slightly longer than broad in *R. calcareus* (Wilmott 1940, 203) cannot be upheld since the figures indicate that it should be more elongated than that of *R. lochabrensis*.

4. For *R. lintoni* part of the diagnosis runs "Calyx juvenilis aliquantum, maturus paululum vel vix longior quam latus, parvus (e.g., $12 \times 9\frac{1}{2}$, $9\frac{1}{2} \times 10$, 13×11 mm.)" (Wilmott 1940, 209). It can only be assumed that the length and breadth figures have been accidentally reversed or misprinted in the second example, since the written description is obviously at variance with this example. Omitting this second example this series falls within the ranges of S_L of both *R. spadiceus* and *R. calcareus*, despite the differences in the wording of the descriptions of the three species.

It must be concluded from the observations above, that the published calyx measurements and descriptions of calyx shape are of exceedingly doubtful value as diagnostic characters for subdivision of *R. minor* L.

INTERNODE LENGTH

Internode length has been mentioned in the diagnoses of each of the *Rhinanthus* species of Wilmott. Although written descriptions of length are given, in only one instance—that of *R. calcareus*—is any measurement given. Owing to the use of terms such as "upper", "lower", and "even below the topmost branches" to define the position of internodes, and of terms such as "short", "long" and "elongated" to describe their length, the meanings of most of the descriptions are obscure.

In order to provide a numerical basis for discussion, every internode on each of the holotype specimens in the Herbarium of the British Museum has been measured.

The following paragraphs are an attempt to demonstrate some of the apparent inconsistencies in the descriptions of various species.

1. The description of *R. calcareus* (Wilmott, 1940, 202) runs "lower internodes about 8 mm. long, those between the intercalary leaves greatly elongated averaging 5 cm. long." It was evident from my measurements that the lengths of the internodes of the holotype specimen increase gradually (with minor irregularities) from the first to the eighteenth. Only two (the third and fourth) could be described as "about 8 mm. long", being 7 and 9 mm. long respectively. I have investigated the "lower" internode lengths of a number of specimens of *R. calcareus* determined by Wilmott in Herb. Mus. Brit. These showed considerable diversity and supported my conclusion that it is not possible to apply this description even to authenticated specimens.

The description quoted above is ambiguous, since it is uncertain whether the word "averaging" is intended to refer to the average for a single plant, or for the taxon in general. The average length for the four internodes "between the intercalary leaves" on the holotype specimen is 4.4 cm. although the longest of these was found to be 5.2 cm. An

investigation of the internode lengths of thirty specimens in Herb. Mus. Brit. was carried out. All these plants had been identified as *R. calcareus*, and the gatherings (from nine different localities) had in most cases been mentioned in one or both of Wilmott's 1940 and 1942 papers. In only three of the thirty specimens was any internode between intercalary leaves 5 cm. or longer, and, in these three, the mean length of these internodes was found to be 4.4, 4.5 and 4.8 cm. respectively. No arrangement of the data from these plants would give an "average" of 5 cm.

2. *R. lochabrensis* is described as possessing ". . . internodes elongated even below the topmost branches, longest between the middle intercalary leaves", but the intercalary leaf numbers are given as "(rarely 1, 2)3(4) pairs" (Wilmott, 1940, 211). If the usual intercalary leaf number for the taxon is 3 pairs it is difficult to see how the two characters are compatible since there can be only one "middle" leaf pair.

3. The inflorescence of *R. calcareus* was described by Wilmott (1940, 203) as "lax". My measurements of the holotype specimens indicate that the mean length of the internodes between the three lowest flowering nodes is *greater* in the cases of *R. spadiceus*, *R. vachellae*, *R. lintoni* and *R. borealis* var. *calvescens* than in *R. calcareus*. It is somewhat difficult to see the reason for the inclusion of the term "lax" in the description of this species.

Other examples in the original thesis indicated similar anomalies in respect of the descriptions of other taxa including *R. spadiceus*, *R. spadiceus* subsp. *orcadensis*, *R. lintoni*, *R. vachellae* and *R. borealis* var. *calvescens*.

The evidence from these investigations indicates that it is by no means certain whether absolute or relative internode lengths were intended in the various diagnoses, and it is evident that whichever one was intended in the diagnoses by Wilmott, it has not been used consistently.

INTERNODE NUMBERS ALONG THE AXIS AND THE CHARACTER OF "INTERCALARY LEAVES"

Descriptions of internode numbers or node numbers which appear in diagnoses of British *Rhinanthus* taxa are in some cases specific, referring to a particular region of the stem, and in others general, referring perhaps to the entire stem. Specific reference to the number of nodes bearing "intercalary leaves" is given in all the diagnoses of British species by Wilmott, and reference to the number of flowers appears in some diagnoses.

There are no references to the total number of nodes in precise terms.

INTERCALARY LEAVES

Intercalary leaves, first named by Sterneck (see Wilmott, 1940, 201), are leaves between the topmost branches and the lowest bracts. Careful investigation of the buds in the axils of intercalary leaves reveals that they are, in most cases, aborted flower buds. Intercalary leaves are thus analogous to bracts, a fact which appears to have escaped previous notice. Simple-stemmed plants may possess pairs of such leaves which will here be referred to as "sterile bracts". Since, however, by definition, intercalary leaves must occur above the topmost branch, it is impossible for a simple-stemmed plant to possess intercalary leaves. As the possible presence of intercalary leaves on unbranched plants has not previously been considered, it will be seen that like cannot always have been compared with like in diagnoses of simple-stemmed and branched species.

Wilmott (1940, 211) in the diagnosis of *R. lochabrensis* gave the stem habit thus "Caulis . . . simplex vel ramis paucis . . ." and the intercalary leaf-pair number as

(1-2-)3(-4)", with no mention of plants without intercalary leaves. The simple-stemmed examples of the species must, however, lack intercalary leaves (in Sterneck's sense). The diagnosis of *R. lochabrensis* is therefore contradictory. If the figure "0" is in fact included in the diagnosis of *R. lochabrensis*, the range of intercalary leaf-pair numbers for the species covers almost the entire range recorded in the literature for British *Rhinanthus*, that is 0-4. The only species recorded as possessing a greater number of intercalary leaves is *R. calcareus*, which is described as possessing "(2-)4-5(-6) pairs" (Wilmott, 1940, 202).

In view of the facts reported above and the fact that a range of intercalary leaf numbers is indicated for each species, it is difficult to find adequate reason for regarding this character as of any great importance in existing taxonomic diagnoses.

FLOWER NUMBER

Several criticisms may be made of the use of this character in the diagnoses of British *Rhinanthus* taxa where it is used by Wilmott, and in other descriptions e.g. those in *Flora of the British Isles*.

The following remarks represent a summary of the more important points presented in the original thesis:

1. It is noticeable that the number 5 is included in the ranges published for each of the British species by Wilmott or Warburg, except in the case of *R. stenophyllus* for which Warburg gives the range 6-12.

2. A specimen on the holotype sheet of *R. spadicus* bears three flowers more than the maximum of five indicated in the diagnosis.

3. Examination of the various holotype specimens indicated that the description of the flower number of *R. lintoni*, that is (2-)3-4(-5), would cover them all.

4. Observations of cultivated plants of *R. minor* indicated that the flower number of *Rhinanthus* is considerably affected by environmental conditions.

There is thus evidence that the range of flower number in *R. minor* is continuous and cannot be of value for subdivision of this taxon.

HEIGHT

Height has been mentioned in diagnoses and descriptions of British *Rhinanthus* species. Fig. 3 shows the published ranges of height for various taxa. The first point which is evident from the figure is that there is a continuous range of heights.

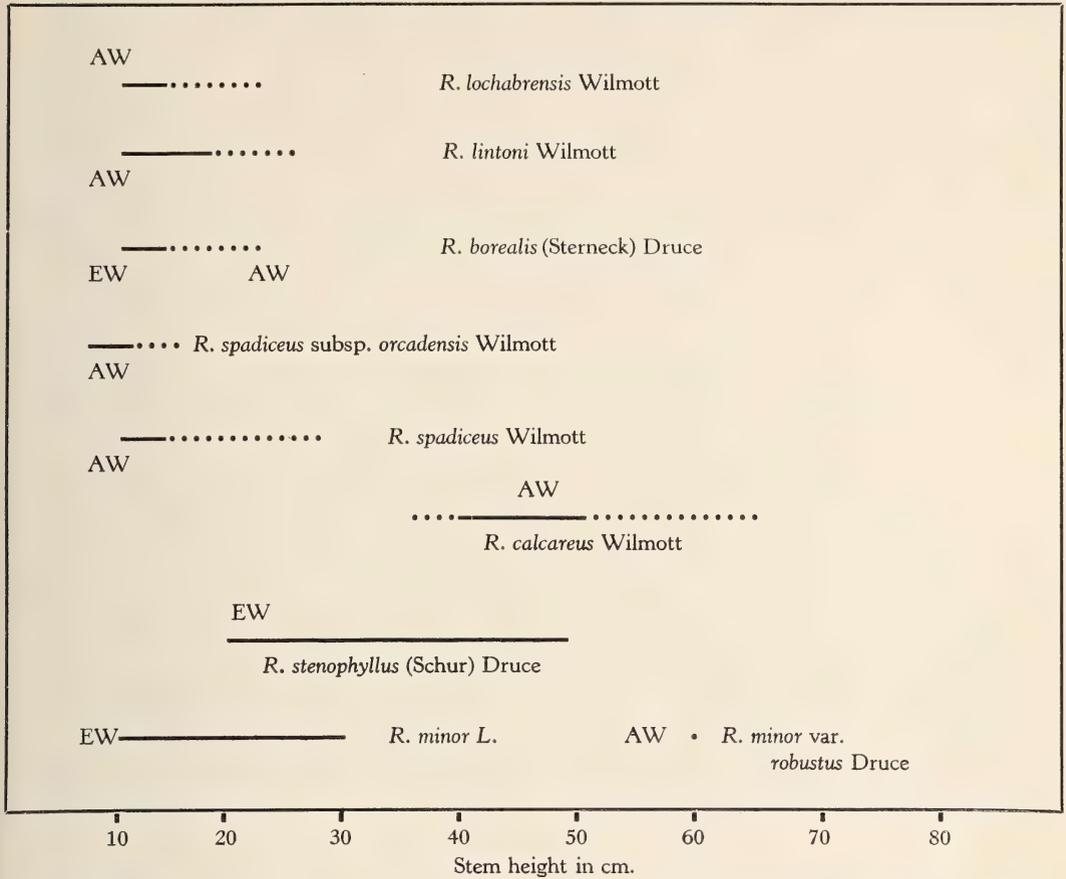
Space does not permit an exhaustive study of height in relation to the taxonomy of *Rhinanthus*, but the following is a summary of results presented in detail in the original thesis.

Height frequency histograms were prepared from data obtained from ten samples (the sample numbers varying from 25 to 72) of *R. minor* from localities ranging between Cornwall and Shetland. These histograms were each consistent with the view that height distribution was approximately normal within each population. The following points emerged:—

1. Two samples with overlapping height ranges (from The Lizard, Cornwall, and Tingwall, Shetland) have a total height range extending almost to the upper limit of the total range of published heights for British species, and *below* the lower limits of this range.

2. The Lizard specimens could not be identified (owing to the width of their leaves) as *R. calcareus* or *R. stenophyllus* and, therefore, do not correspond with any of the published diagnoses for British *Rhinanthus*.

Fig. 3. Published height ranges for British *Rhinanthus* species.



Note—Continuous lines indicate the published “ typical ” ranges whilst dotted lines indicate exceptional (?) extensions of the range.

Key— AW = Range given by A. J. Wilmott, 1940.
EW = Range given by E. F. Warburg, 1952.

3. A sample from a population at c. 1,400 feet on Ben Nevis, Inverness-shire, was found to have a majority of plants with pubescent calyx, and a modal height of 10 cm.; this is at the lowest limit of the published height range for any of the British species with pubescent calyx, and the lowest limit of the height range in this sample (4 cm.) was well below the lower limit of any of the published ranges for these species.

4. Each of the ten samples mentioned above possessed a different modal height, these modes forming a gradually ascending series between 10 cm. and 43 cm. There was a continuous range of height between the shortest and the tallest plant recorded in this investigation.

The final conclusion must be that there is a continuous height range in British *R. minor* L., and further, that the subdivisions of this range bounded by “ round numbers ” are not valid for discrimination of taxa.

BRACT SHAPE AND LENGTH

A bract may be defined as a leaf in the axil of which arises a flower or branch of an inflorescence. Warburg (1952, 888) wrote that intercalary leaves (see p. 107) “ are often

transitional between the lower leaves and bracts in shape and tothing" and he defined the bracts used in his descriptions of species as excluding "the two lowest pairs which are often transitional to the leaves." There appears to be a more or less gradual change in the shape of leaves in the widest sense of the term (i.e. including bracts) from the base to the apex of the stem in any *Rhinanthus* plant. In general, there is a widening of the base of the leaves and an increase in the divergence and length of the leaf teeth associated with the flowering part of the axis. The leaves of a specimen with numerous flowering nodes are usually triangular in the lower part of the inflorescence, and become more ovate towards the apex of the inflorescence. Frequently only one flower is borne on a node, but there is no great difference in the shape of the two bracts at this node (although sometimes the sterile bract is slightly the smaller). In the lower part of the inflorescence, flowers may be borne in the axils of bracts which are almost identical in shape to the sterile bracts (intercalary leaves) which occur below them. Sterile bract-pairs in the lower part of the inflorescence should be included in the orthodox descriptions of bract shape, since, using Warburg's system mentioned above, it is possible, for example, that comparison of the third bract pair of an inflorescence without "intercalary leaves" might be made with the fifth bract pair of an inflorescence with two intercalary leaf pairs. Such a comparison is hardly justifiable. In British *Rhinanthus* it appears that the main differences in shape indicated between the bracts of different species are such as occur between successive bracts in a single inflorescence of a well-developed plant.

My observations on cultivated plants have indicated that environmental factors influence the number of flowers produced by *Rhinanthus*, and that plants dwarfed, for example, by cultivation without a host plant, produce fewer flowering nodes than luxuriant specimens, and may fail to produce the more ovate bracts characteristic of the upper part of the inflorescence, although genotypically capable of doing so. It is, therefore, unwise to place too great an emphasis on bract shape as a diagnostic character for subdivision of *R. minor* L.

LEAF MEASUREMENTS

Careful study of the type specimens and of field populations of *Rhinanthus* indicated that the range of leaf measurements in *R. minor* is continuous. The ranges published by Wilmott in his diagnoses are small, and in some instances smaller than the range shown by single local populations. Discrepancies occur between the holotype specimens and descriptions in several cases; for example, a leaf of the holotype of *R. vachellae* was found to be 3 mm. wide, 1 mm. greater than the figure published in the diagnosis; similarly a leaf of the holotype of *R. lintoni* was found to be at least 2 mm. broader than the 3 mm. indicated in the diagnosis, despite the fact that shrinkage in drying has undoubtedly occurred.

It was concluded after a detailed investigation (reported in thesis) that no importance can be attached to the published leaf measurements for discrimination of British *Rhinanthus* taxa.

LEAF SHAPE

From the published diagnoses and descriptions of leaf shape in British *Rhinanthus* taxa, considerable differences between taxa might be expected. From the remarks of Sterneck (1901, 107-8), translated by Marshall (1903), it is evident that a very considerable variation may occur even within a single *Rhinanthus* population. My observations on *R. minor* populations (see thesis) strongly support this. Variation in the shape of leaves

from the base to the apex of the stem was noted by Chabert (1899), who remarked that the lower leaves were often shorter and more obtuse than the upper ones. My observations indicate that different populations are often characterised by different numbers of nodes below the inflorescence, and that certain phases of leaf shape, present in plants with numerous internodes, are omitted from plants with fewer nodes. It might, therefore, not be comparing like with like, when the upper leaves of plants with few nodes are compared with those of plants with numerous nodes. It would, therefore, have been preferable in orthodox taxonomic diagnoses to have compared node numbers rather than leaf shapes, whose differences are subjectively determined and which depend partly on factors (e.g. position on the stem) which have only been arbitrarily defined in the literature.

Measurement of the holotype specimens of Wilmott's seven taxa indicates that the topmost stem leaf (excluding intercalary leaves and bracts), which was taken as a standard, tapered from near the base in each case. The diagnoses of *R. calcareus*, *R. spadiceus* and *R. lintoni*, which indicate that the leaves are "linear" for the first species and "linear-lanceolate" for the second and third, cannot be accepted.

In view of the considerable variability in shape which in some populations is much greater than the entire range of the holotype specimens under discussion, it is doubtful whether species may be diagnosed by such a character, the variation of which is probably due in part to segregation of factors affecting allometry and to genetic or environmental control of the number of nodes below the first bracts. It is not surprising that some populations may appear more uniform than others (e.g. a sample from Ben Lawers had a very small range of shape (see thesis)), since (excluding the effects of any mutation) any genetically controlled variability will depend ultimately on that inherent in the original ancestor(s) (which may be very few) of any spatially distinct population.

If this brief investigation has demonstrated the inadvisability of attempting to distinguish British *Rhinanthus* species on the character of leaf shape it will not have failed in its object.

PUBESCENCE

The character of pubescence of various organs has been mentioned in a number of taxonomic diagnoses of British *Rhinanthus* species. Soó (1929, 82) considered the pubescence of the calyx to be very important. He distinguished four main types of calyx pubescence, only one of which, "the quite short-hairy" type, occurs in Britain according to Wilmott (1942, 372). The description of hairiness refers to the calyx surfaces, excluding the margin which appears to be hairy in all British forms. The pubescence of organs other than the calyx does not appear to have been regarded by taxonomists as of such importance as that of the calyx. A brief mention of such considerations and assessments of their importance will now be made, with a more detailed discussion of calyx pubescence.

Stem: the descriptions of stem pubescence for British *Rhinanthus* species are somewhat vague in the few cases where they are given in the literature. It might be noted, however, that environmental factors considerably influence the apparent degree of pubescence of the stem. Plants dwarfed, e.g. by cultivating them without a host plant, appear more pubescent on the stem than larger specimens with longer internodes.

Leaves: *R. lintoni* is the only British species for which a record of distinctive leaf-pubescence exists. The hairs on the "midrib (and sometimes veins) beneath" are described (Wilmott, 1940, 210) as "longer." It is interesting to note that the holotype specimen of *R. lintoni* is on a sheet in Herb. Mus. Brit. with other specimens of the original gathering, some of which are labelled "*borealis*" with the signature of the late A. J. Wilmott. It seems probable that the presence or absence of the slight elongation of hairs indicated in

the diagnosis could easily be due to simple allelic differences between members of a single population, and that it is not a character likely to be associated with cross-fertility barriers within such a population. It is further obvious that it was necessary to select individuals with particular combinations of characters from the type population in order to describe them as a new species.

Bracts: in British *Rhinanthus* the scabrousness of the foliage decreases towards the apex of the inflorescence, the upper bracts of plants with numerous flowers being almost glabrous. The descriptions of bract pubescence in British literature must be considered in relation to this fact, since it might be expected that all the bracts of few-flowered forms would exhibit pubescence; it must be remembered that these may be comparable with the lower bracts only of larger specimens. In the light of these remarks, it is evident that no significant references have been made with regard to bract pubescence in the diagnoses of British species.

Calyx: Wilmott appeared to recognise five taxa with a shortly pubescent calyx surface in the British Isles; these are *R. borealis* (Sterneck) Druce, *R. lintoni* Wilmott, *R. lochabrensis* Wilmott, *R. vachellae* Wilmott and *R. borealis* var. *calvescens* Wilmott. It is evident from the literature that considerable similarities exist between some plants with a pubescent calyx-surface and others without, and that there are some intermediate forms e.g., *R. borealis* var. *calvescens* (see p. 103; and Wilmott, 1940, 209).

It might be argued that when there exists a complete series (such as Wilmott himself indicated) between two extremes in a single locality, it is unwise to take a sample midway between these extremes and name it as a new variety.

R. vachellae was described by Wilmott in 1948 as "another British *Rhinanthus* with pubescent calyx". Some of his doubts about this taxon have been indicated on p. 103.

Chabert, in 1899, wrote that the character of pubescence of the calyx in *Rhinanthus* varied with age . . . "The calyx is very accrescent between the opening of the flower and the maturation of the seeds, its surface becoming doubly and occasionally triply extended. As it does not give rise to new hairs, those which exist become very much less dense and in consequence are relatively smaller in number. . ." (translated). Marshall, in a letter to Linton (1903), indicated another type of alteration in pubescence . . . "In some of my flowering specimens of *R. borealis* the whole surface of the calyx is densely pubescent. As they grow old the calyces lose their hairs gradually, at last becoming almost glabrous." I have confirmed these observations, since both phenomena occurred in Swedish *R. minor*, which was cultivated in England in 1955. Any description of calyx pubescence, should, therefore, indicate the age of the specimen. Apart from such disadvantages, if, as Wilmott (1948, 84) wrote, ". . . the hairy calyx may be a variable character in some species of *Rhinanthus*", it may be argued that it cannot be a reliable character by which to separate one species from another, and it cannot be of such fundamental importance in the taxonomy of *Rhinanthus* as Soó (reported by Wilmott, 1942, 372) thought.

Various facts indicate that the glabrousness or "quite short hairy" pubescence of the calyx may depend on a pair of allelomorphs, which can segregate and re-combine with numerous combinations of genes, affecting other taxonomic characters. The description of populations of *R. groenlandicus* by Ostenfeld (1901, *Bot. Faroes*, 51-55), quoted by Wilmott (1942, 371), shows "that among a large number of Arctic specimens there are always some with a hairy calyx, but the greater part with glabrous, though the specimens do not otherwise differ from each other in any respect." Dr. N. Hylander, in a letter to the present writer, described collections in the Herbarium of Uppsala Universitets Institution För Systematic Botanik which came from "Northernmost Finland" and "Northernmost Norway" thus: "it must be stressed, that in many of these collections only some specimens have pubescent calyx, whilst the rest have glabrous; apparently both types

occur together in one and the same population without any ecological differentiation at all." The considerable similarity recorded by Wilmott (1948, 84) between *R. vachellae* and *R. stenophyllus* and *R. spadiceus* except in the pubescence of the calyx of the former species might also be taken to indicate that pubescence of the calyx may sometimes represent merely an allelic difference between otherwise similar forms.

Although *R. borealis* was described as a "circumpolar Typus" by Sterneck (1901, 333), and although there is evidence that the character of pubescent calyx is associated with mountain or boreal habitats (i.e. in Britain it is only recorded from Scotland and the northern islands in the literature, whilst specimens sent to me by Mr. Evan Roberts from Moel Siabod, Wales, at 2,000 feet indicated that the character occurs in the Welsh mountains), it is not necessarily at great selective advantage in such regions. This is indicated by the remarks of Hylander above and the record of *R. borealis* subsp. *salmonii* Soó (a taxon with glabrous calyx surface) at 2,000 feet (Wilmott, 1942, 373). It is interesting to note that the character of "shortly hairy calyx" occurs in *Rhinanthus* of non-montane regions in the New World and extends, according to Sterneck's map (1901, Taf. 111), as far as the southernmost limits of the genus; here it occurs in *Alectorolophus kyrollae* Chabert and *A. pacificus* Sterneck. The reasons for the present geographical and altitudinal distribution of forms with shortly hairy calyx and those with glabrous calyx remain obscure, as their ecological tolerance ranges appear to overlap considerably.

Corolla: pubescence of the corolla appears to have been mentioned only in connection with *R. vachellae* amongst the British species. The corolla of *R. vachellae* was stated by Wilmott (1948, 84) to be much more pubescent than that of *R. lintoni*; no mention of this character appears in the diagnosis of *R. lintoni*. Examination of the holotype specimens does in fact indicate that the lateral surface of the hood only of the one well-preserved corolla of *R. vachellae* on the type sheet has somewhat more conspicuous pubescence than any of the other holotype specimens of Wilmott's species. However, in view of the difficulties in estimating degree of pubescence (which appears to vary continuously) it is not possible to place much reliance on such subjective comparisons for identification of critical species.

Conclusion Regarding Pubescence

The ultimate conclusion must be that differences of pubescence in *R. minor* L. need considerably more study before their value in the subdivision of this taxon can be assessed.

PIGMENTATION

From diagnoses of *Rhinanthus* species it would often appear that differences of pigmentation have been regarded as important. The colour of the corolla teeth has been used in most specific diagnoses and has, in some cases, led to controversy (see Wilmott, 1942, 363). The pigmentation of stem, bracts and calyx has been used in taxonomy. Wilmott, for example, wrote of *R. minor* "The stems may be quite green, or black-striolate, or suffused with some form of (reddish to violet and blackish) anthocyanin", and "many . . . forms of *R. minor* tend to be suffused with purple-violet on the bracts, calyces, and even stems." He suggested that, as these colorations had been used in descriptions, the variation in the field should be noted in case these colorations should prove to be associated with morphological differences, and that the colour of the corolla needs study from week to week to see if it changes.

The following is a brief summary of the main points which have emerged from observations on cultivated plants and natural populations.

The colour of the corolla tooth in a single Kentish population of *R. minor* varied

from plant to plant, Spinel pink 0625/2, Aconite violet 937/3 and Dauphin's violet 039/1 (the colours are from Wilson's 1938 Colour Chart) being among the colours recorded.

The teeth of successive corollas on a single plant may vary between white and violet in *R. minor* (and in *R. serotinus*). The violet teeth of a single corolla may fade almost to white before the corolla falls. The coloration of the corolla tooth and striolation of the stem are genetically controlled characters which are not necessarily linked. Rubescence of the stem, bracts and calyx, stem striolation and in some cases pigmentation of the corolla teeth appear to be enhanced by dry conditions.

In view of the evidence presented it is concluded that corolla tooth colour, striolation of the stem, and rubescence of the upper parts of the plant are not good taxonomic characters for discrimination of *Rhinanthus* species.

The "treacle-brown" colour (see Wilmott, 1942, 368) of the corolla in *R. spadicus* is due to the development of reddish or purple anthocyanin in epidermal cells of the corolla (which also contain yellow plastids) as it matures. A corolla will appear "treacle" or "fuscous spotted" (cf. *R. perrieri* Chabert) depending on whether a majority of cells contain anthocyanin or whether this pigment is mainly confined to more particular groups of cells. Both conditions may occur in a single field population, and the spotted condition is probably often a transitional stage to the completely treacle corolla. The exact shade of the mature corolla depends on the concentration and colour of anthocyanin present. Similar development of pigment in the corolla occurs in other *Rhinanthus* taxa and the process has been followed in Swiss *R. cf. angustifolius* C.C. Gmel. which was cultivated in London in 1955. The corollas of two plants were Dresden Yellow 64 (Wilson's Colour Chart standard) at the time of opening. The corollas became mottled with red on the lower lips soon after they had expanded fully, and finally became orange in colour before becoming detached from the plant. This coloration had previously been observed in the field at the locality (near Zermatt) from which the seeds were collected in 1953. Development of diffuse anthocyanin pigmentation of the corolla is undoubtedly an inherited character in *Rhinanthus*, but in view of the fact that I have observed it in taxa as distinct as *R. serotinus* (Swiss plants), *R. cf. angustifolius* (Swiss) and *R. minor* (Swiss and British) it seems unlikely that this would be a valuable character for the subdivision of one of these taxa. This is borne out by the fact that I have observed the character in various combinations with other characters within *R. minor*, e.g. in plants with glabrous calyces (Malham, Yorks; Shetland; Orkney; Dover, Kent) and plants with pubescent calyces (Ben Lawers, Perthshire).

A variable number of black or brown anthocyanin spots occurring on some *Rhinanthus* corollas have been found to be genetically controlled, although environmental factors have some effect on their intensity. They occur in *R. minor*, *R. cf. angustifolius* and *R. serotinus*.

The conclusion must be that the varying anthocyanin pigmentation in *Rhinanthus* does not provide any sound taxonomic character.

CONCLUSIONS AND DISCUSSION

It has been shown in the first part of this paper that British *Rhinanthus* may be satisfactorily split into two taxa by the use of floral characters only. These taxa agree with the original diagnoses of *R. minor* L. and *R. serotinus* (Schönh.) Oborny, respectively. The latter species has not been considered in detail in the present paper.

The group of plants possessing the corolla characters of *R. minor* has been divided into a number of species, including several supposedly endemic British ones, described by Wilmott. The investigations recorded in the present paper indicate that descriptions

of these species are unsatisfactory in a number of respects : some of the descriptions fail to agree with the type material : inconsistencies and ambiguities have been discovered in the descriptions of some individual characters in the various diagnoses : some taxonomic characters have been shown to vary within single populations; some characters have been mentioned in the diagnosis of one species and not in another, and so on; the individual conclusions need not be repeated here. It is evident that division of *R. minor* L. into species has not been satisfactory with regard to British forms. Since one of the main objects of orthodox taxonomy must be to provide a method for recognition of similar forms, it is essential that the descriptions of such forms shall be mutually exclusive; this necessitates, especially in the taxonomy of critical groups, a precision in diagnosis which has been lacking in descriptions of *Rhinanthus* under discussion.

It is evident from my investigations that existing diagnoses do not cover all the British forms of *Rhinanthus*, and it appears that each *Rhinanthus* population might have a combination of phenotypic characters which renders it distinct from every other population. This might be expected if, in fact, the total British *R. minor* population included various combinations of genetically controlled characters, some of which might be modified by environmental influences. It would require independent assortment of genetic factors controlling only four such characters (e.g. calyx pubescence, habit, leaf shape and shape of corolla teeth) for sixteen "species" to be produced. If certain individuals or populations became genetically isolated, for example, by transference of seed to new localities, different environmental influences acting on the various populations might allow genetic drift to take place along different paths (the variability of an isolated population would depend in the first instance on the homozygosity or otherwise of the initiator(s) of that population). This situation might lead to production of forms differing to a lesser or greater degree, whilst any subsequent breakdown of barriers to outbreeding between isolated populations might give rise to further phenotypic variability. The complex series of phenotypes which undoubtedly exists in British *Rhinanthus* might have arisen in this way. Attempts to provide a name for every phenotype would result in a very great multiplicity of names, as has been pointed out by Marsden-Jones and Turrill (1954, 183) in relation to their studies on *Centaurea*.

This paper has been an attempt to assess the value of existing descriptions of British *Rhinanthus*. It has become evident that the diagnoses of certain species cannot be used with any degree of confidence for identification of even the type specimens.

It is relevant to note here that a number of *Rhinanthus* populations have been examined cytologically and that no evidence has been found of varying chromosome numbers either within *R. minor* (a number of forms have been investigated) or between *R. minor*, *R. cf. angustifolius* and *R. serotinus*. All so far examined were found to possess $2n = 22$ chromosomes (original thesis and Hamblen, 1953 and 1954). The diploid complement of 14 large and 8 much smaller chromosomes is somewhat unusual; the fact that it is common to all *Rhinanthus* forms so far examined may be taken as evidence of their recent evolutionary divergence.

My investigations lead me to the conclusion that the type specimens of the British *Rhinanthus* taxa described by Wilmott merely represent minor genetic variants, and should all be regarded as belonging to the species *R. minor* L.

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THE HISTORY OF *SYMPHYTUM ASPERUM* LEPECH. AND *S. × UPLANDICUM* NYMAN IN BRITAIN

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Symphytum asperum Lepechin was, according to Aiton (1810) introduced in 1799 by Conrad Loddiges. Loddiges' nursery at Hackney was purchased from Joseph Busch, who had been appointed head gardener at the Palace of St. Petersburg, and who between 1790 and 1801 sent to Conrad Loddiges several species of *Symphytum* including *S. asperum*.* During the first half of the 19th century *S. asperum* was grown as a fodder plant, but to what degree is difficult to determine owing to confusion with *S. × uplandicum*. As a naturalised plant *S. asperum* is extremely rare and I have been able to confirm only about 20 records extending over 120 years. It is a less persistent species than most comfrees and appears to have died out in most of its recorded localities in Britain.

Tutin (1956) suggests that the introduction of *S. asperum* and its hybridisation with the native *S. officinale* gave rise to *S. × uplandicum* in this country. That such a hybridisation may have taken place in Britain is not disputed; indeed there may be some slight grounds for supposing that *S. × uplandicum* in the Oakford Valley near Bath had such an origin, since *S. asperum* was collected in that locality in 1834 and 1868 by C. C. Babington and T. B. Flower respectively. It seems, however, to have disappeared by 1879. C. Bucknall searched for it without success during 1910-12, but he did find *S. × uplandicum* growing abundantly and hybridising freely with *S. officinale*. Against the view that *S. × uplandicum* arose there as a result of a cross between *S. asperum* and *S. officinale* is the fact that although there is great variation displayed between one colony of *S. × uplandicum* and another none of them shows any variation in the direction of *S. asperum*. So far as my knowledge goes there is no record of *S. × uplandicum* having been found growing in this country in the company of the parent species.

In the Kew Herbarium is a specimen of *S. × uplandicum* collected by Forbes Young at Cobham Lodge, Kent, in 1827, which may have been supplied by Loddiges, and which seems to be the first record of its cultivation in Britain. The earliest record of it as a naturalised plant is in 1861 from Marlborough, Wilts. Earlier records from the Oakford Valley quoted by J. W. White in his *Flora of Bristol* refer to Babington's and Flower's records of *S. asperum*.

Lawrence D. Hills (1954) in dealing with the history of the Russian Comfrey shows that *S. × uplandicum* has been introduced as a forage crop on many occasions during the past 100 years. It was probably also introduced during the first half of the 19th century under the erroneous name of *S. asperinum*. The cultivation of Comfrey seems to have become very popular from 1870 onwards, when Henry Doubleday of Coggeshall, Essex, imported *S. × uplandicum* from Leningrad (then St. Petersburg). The figure in Curtis' *Botanical Magazine*, plate 6466 (1879) under the name of *S. peregrinum* was drawn from plants presented to Kew in 1875 by Thomas Christy, who was associated with Doubleday in his efforts to popularise its cultivation. Several seedsmen took up the distribution of the

*The early editions of the catalogues issued by Conrad Loddiges and Sons have not been traced, but the 11th edition of 1818 lists the following: *Symphytum asperinum*, *S. caeruleum*, *S. coccineum*, *S. patens*, *S. tauricum* and *S. tuberosum*. The first is synonymous with *S. asperum*, of which *S. caeruleum* may have been a variety. *S. coccineum* was presumably the crimson-flowered form of *S. officinale*, and *S. patens* may have been the purple-flowered variety of *S. officinale* or the plant now known as *S. × uplandicum*.

plant, including Messrs. Sutton of Reading, who continued to supply it until 1896. In 1900 Messrs. Webster of Stock, Essex imported it from Russia and they and other nursery-men still carry stocks. These and other introductions from Russia and elsewhere are undoubtedly the chief, if not the sole, origin of *S. × uplandicum* in Britain.

In spite of its hybrid origin *S. × uplandicum* is apparently a fixed hybrid and any variation it shows is due to its back-crossing with *S. officinale* and more rarely, and perhaps less certainly, with *S. asperum*. Populations of *S. × uplandicum* known to me, unless growing in close proximity to *S. officinale*, show remarkable uniformity, and plants grown in Cardiff from seed collected from a large population in Pembrokeshire showed no variation from the parent plants. It was this uniformity and absence of segregation which led the late C. Bucknall and others to consider it a good species.

The present known vice-comital distribution is 1-4, 6-9, 11-14, 16, 17, 19-24, 28-30, 32-37, 40-52, 54, 55, 57-59, 61-64, 67, 69-71, 73, 77, 78, 82-85, 88-90, 92, 93, 95, 96, 101, 105, 111, 112. H. 1, 2, 7, 12-16, 18-21, 23, 25, 27-30, 33-40. C.

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MINT NOTES

By R. A. GRAHAM

VIII. A NEW MINT FROM SCOTLAND

In 1912, G. C. Druce submitted to Briquet, in Geneva, a mint which he had collected in Glen Ogilvy, Forfar, v.c. 90. This was returned with the name *M. villosa* Huds. var. *sapida* (Tausch) Briq. *forma valde lanigera*, and this varietal epithet was accepted without question as applicable to the Scots mint. The exactitudes of nomenclature are irrelevant, but Briquet apparently adopted this combination as a later substitute for his earlier (1891) *M. × niliaca* Juss. ex Jacq. var. *sapida* (Tausch) Briq., and Fraser continued acceptance of the epithet *sapida* in the latter, more correct, combination. *M. sapida* Tausch was itself originally published as *nomen nudum*, being later validated by Braun (1890, 377). My suspicions of the correct application of *M. sapida* Tausch ex H. Braun, in any grade, to our Scots mint (Graham, 1953, 109; 1955, 281) were recently confirmed when Tausch's original specimen—apparently the holotype—was received on loan from Brussels. Tausch's mint has little resemblance to our plant: it is perhaps *M. × niliaca* var. *villosa* (Huds.) Fraser (*M. longifolia* × *rotundifolia*) to which Briquet in due course referred it (1896, 679).

It is possible that Briquet did not intend *sapida* to apply to the Glen Ogilvy mint. During a visit to the Geneva Conservatoire in 1947 I was able, due to the kindness of Professor Baehni, to examine many of Briquet's mints, and amongst them was a duplicate of the Glen Ogilvy plant, named by Briquet *M. villosa* var. *nemorosa* (Willd.) Briq. On the other hand, another mint, from Wolvercote, Oxon, (v.c. 23), named by Briquet as *sapida* in the Conservatoire, is given by him, on its returned duplicate, the name *M. × niliaca* var. *halleri* Briq. (this Wolvercote mint is in fact *M. × niliaca* var. *villosa*). The possibility of a muddle in returning the names is, however, rather dispelled by the fact that Briquet applied Tausch's epithet to yet another mint, from Haute Savoie, and this latter, although unlike Tausch's specimen, is reasonably close in characters to the Glen Ogilvy plant, differing chiefly in having far more leaf serratures and a greener upper leaf surface. But here again, the tangle is largely irrelevant to the issue at hand: *M. sapida* is wrongly applied to the Scots mint, and in view of this it seems desirable to provide a new name to replace the erroneous, existing one. Extensive consultation in continental literature and among continental specimens has failed to produce a name (in any grade) that seems safely applicable to our plant, and although a name may possibly be one day found among the remoter recesses of the mass of continental mint nomenclature, it is best that a new name be provided whereby our mint may be immediately known. Apart from a rather unsatisfactory specimen, apparently from Kent (1820, *Blake* (OXF)), I cannot remember seeing an example from anywhere other than Scotland, therefore the specific epithet offered below would seem to be apposite.

Mentha scotica R. A. Graham, *species nova* *M. longifoliae* (L.) Huds. *affinis sed foliis latioribus oblongioribus minus acutis, serraturis minus altis et minus acutis valde distinguitur*. *Holotypus*: Glen Ogilvy, near Glamis, Forfar, v.c. 90, 2 Oct. 1926, R. & M. Corstorphine (K).

Mentha venusta, *facie ± grisea, odore ingrato. Caulis molliter tomentosus infra glabrescens, ramosus. Folia oblongo-elliptica vel oblonga vel ovato-oblonga, 3.2 — 8.7 × 1.7 — 4.2 cm., sessilia vel ad 2 mm. petiolata, erugosa, apice ± obtusa, basi*

truncata vel *subcordata*, supra *griseo-viridia* vel \pm *caeruleo-viridia* pilis mollibus brevibus appressis vestita, infra *griseo-alba* dense et molliter tomentosa pilis simplicibus, dentibus parvis non salientibus \pm *irregularibus* ad 1 mm. sed plerumque c. 0.5 mm. (vel minus) altis serrata. Inflorescentia spiciformis racemosa terminalis densa, 2 — 5 cm. longa c. 1 cm. crassa. Calyx campanulatus 2.25 — 2.75 mm. longus dentibus apice \pm setaceis plumoso-ciliatis 0.75 — 1 mm. longis auctus. Corolla punicea vel puniceo-lilacina 3 — 3.25 mm. longa lobis apice \pm rotundatis 1.25 — 1.5 mm. longis. Stylus exsertus c. 4 mm. longus. Stamina inclusa.

This attractive mint is characterised by its greyish-white leaves with a bluish tinge on the upper surface, whiter below, by their breadth, by their small and shallow serratures, by the soft indumentum which clothes the whole plant, and by its unpleasant smell which is somewhat reminiscent of cats. The leaves attain 11×4 cm. in strong examples, the petioles may be as much as 4 mm. long (though usually much less), and the length of the corolla may be as much as 4 mm. with lobes 2.25 mm. Otherwise it is a markedly unvarying mint. Despite Fraser's description (Fraser, 1927), I have been unable to detect a single branched hair on any part of the plant. The primordial leaves are, rather surprisingly, glabrous and green on both surfaces.

The origin of our new species has yet to be deduced. It is presumably a clone that may have arisen locally. Briquet and Fraser were content to include it in the *M. \times niliaca* (*M. longifolia* \times *rotundifolia*) group of hybrids, but it is difficult, especially in the absence of leaf rugosity and branched hairs, to see any influence of *M. rotundifolia* in it. Professor Tutin, to whom I am indebted, arranged for the chromosomes to be counted, and the resulting figure of $2n = 44$ is a little difficult to account for unless (as Dr. Morton has suggested to me) it represents an error for $2n = 42$ —which might be taken to suggest a backcross of an F1 offspring of *M. longifolia* ($2n = 48$) \times *rotundifolia* ($2n = 24$) with the former parent. Aneuploidy is also a possibility. It is clearly advisable to await further cytological investigation, and for the time being the only possible grade is that of *species*. It is worth noting that despite reproduction by readily-spreading subterranean runners, fertile seed is produced and has been germinated.

M. scotica is recorded from low-lying parts of E. Perth (v.c. 89) ; from Forfar (v.c. 90) ; and from Elgin (v.c. 95). It is by no means uncommon along burns in Angus, the locality by the road-bridge at Glamis being well-known. Further collecting will establish its exact distribution and frequency, but it probably extends from Perth to Angus, continuing through the Mearns to coastal Aberdeenshire, and thence westwards along the southern side of the Moray Firth. It has been distributed on several occasions through the Botanical Exchange Club (1912, 1937, 1952 cult., 1954), and has been variously named as *M. longifolia*, *M. sylvestris* L., *M. candicans* Crantz and *M. mollissima* Borkh. As a result, specimens are fairly widespread among our national herbaria and in private collections. Records checked during preparation of this paper are as follows:—

Mid Perth, v.c. 88 ; Dunbarney, 1906, Wilson (K ; OXF ; herb. R. A. Graham 5064) ; Banks of R. Tay below Perth, 1871, Drummond-Hay 803 (OXF) ; Banks of R. Tay, 1865, Sim (K).

Forfar, v.c. 90 ; Glen Ogilvy, 1926, Corstorphine (K) : 1912, G. C. Druce (K ; OXF ; herb. R. A. Graham 5107) : 1924, Wilmott (BM) : Glamis, 1937, Still (BM ; herb. R. A. Graham 3976) : 1937, Wallace (K ; OXF) : 1876, Drummond (K) : 1947, Reching (BM) : 1957, Graham & Harley (herb. R. M. Harley) : near Parkhill, Arbroath, 1951, Duncan (herb. R. A. Graham 3978) : McClintock (herb. R. A. Graham 3977) : 1954, Duncan (BM) : Netherton, by the South Esk, 1926, Corstorphine (K) : by Meikle Coull, near Tannadice, 1957, Graham & Harley (herb. R. A. Graham 5176 A and B).

Elgin, v.c. 95 ; Forres, 1898, E. S. Marshall (BM) : Brodie Burn, Forres, 1898, Shoolbred & E. S. Marshall (OXF ; herb. R. A. Graham 5065) : Moy Burn, Forres,

1953 *McCallum Webster* (herb. R. A. Graham 3973) : Muckle Burn, above Whitebridge, 1957, *McCallum Webster* (herb. R. A. Graham 5427). In Angus I have also seen this mint near Noranside, and by Maulsden, near Brechin.

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It is not proposed to supply a full and lengthy list of literature references. The following are, however, among the more important works consulted, together with other references immediately relevant to the foregoing text.

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A NEW HYBRID SEDGE

By P. M. BENOIT

On the 24th June 1954, when I was collecting specimens of *Carex punctata* Gaud. near Barmouth, Merioneth (v.c. 48), I noticed a curious plant which differed conspicuously from that species in having purplish-brown female glumes, similar to those of *C. binervis* Sm. As it seemed interesting, I made a note of its location and collected only the two stems which it bore, leaving the basal part in the hope that more stems would be produced in subsequent years.

Examination of these specimens showed that they possessed a combination of *binervis* and *punctata* characters and were sterile ; also the plant is the only one of its kind, and although I did not see *C. binervis* near it in the first place, I found later that *C. binervis* and *C. punctata* actually grow together there in some quantity. It is therefore reasonable to assume that the plant is a hybrid of these two species. Mr. E. Nemes, of the Royal Botanic Gardens, Kew, to whom I sent the specimens, agrees with this view. Such a hybrid has apparently not been recorded before.

Ecological isolation no doubt usually prevents the parent species from hybridising. *C. binervis* is characteristic of moors, the drier parts of bogs, acid pastures, and similar habitats on acid soil ; *C. punctata*, of wet maritime habitats, especially rock crevices and the upper parts of sandy salt-marshes. It is interesting to note that my plant grows on a heathy rock near the shore, a place where the habitats of the parents meet. Associated species are : *Carex demissa*, *Erica cinerea*, *Hedera helix*, *Hypericum pulchrum*, *Molinia caerulea*, *Rosa canina*, *Solidago virgaurea*, *Succisa pratensis*, *Veronica officinalis*, *Bryum alpinum*, *Campylopus atrovirens* and *Saccogyna viticulosa*.

The plant produced four stems in 1955 ; one of them was eaten through when young, but the remainder reached maturity and were gathered. Although apparently healthy it did not produce any in 1956—probably on account of the dry spring, following the very dry summer of 1955. The original specimens were shown at the Society's Exhibition Meeting of the 27th November 1954.

A description follows.

Carex binervis* × *punctata

Rootstock, base of stem and basal leaves not collected. *Stems* 65-70 cm. in height, c. 1.5 mm. thick below. *Leaves* 3-4 mm. wide, flat, the basal (observed in the field) about half as long as the stems. *Terminal (male) spike* 1, occasionally with a much smaller one at its base, erect, 'pedunculate', 25-35 × 2.5-3 mm., ellipsoid-cylindric, light brown, not hoary with the persistent remains of filaments. *Male glumes* c. 4.5 mm., obovate-oblong, erose-ciliate and very obtuse to emarginate at the apex, tapered to the base, colourless, to pale yellowish-brown above, with a pale purplish zone on each side of the stout pale or greenish midrib, which is very slightly excurrent in only the uppermost glumes of the spike. *Stamens* remaining enclosed within the glumes ; the *anthers* c. 2.5 mm., slender, indehiscent. *Lateral (female) spikes* 3, usually very distantly spaced especially below, erect or rarely the lowest nodding, 12-25 × 5-7 mm., shortly cylindric, ± tapering upwards and abruptly contracted into the peduncle (a spike having its most spreading utricles at or near its base and no odd florets on the peduncle), often with a few male florets at the

top ; *peduncles*, uppermost \pm included, the others exerted 10-45 mm. ; *bracts* usually falling far short of the top of the stem, grading from the lowest which are long and leaf-like, with a long sheath, to the uppermost which are with or without a very short blade and with a very short sheath. *Female glumes* 2.5-3 mm., ovate, obtuse, pale purplish-brown, to yellowish-brown above and at the margin, with a stout green midrib which is rough on the back and excurrent in a short mucro (in the lowest glumes up to a quarter of their length). *Utricles* spreading at 40-70°, 3.5-4 \times c. 2 mm., ovate with rounded sides and base, \pm compressed-trigonous with very sharp lateral angles when fresh, flat on account of the undeveloped nut and faintly nerved or wrinkled when pressed, shining, punctate, pale green above to whitish below, occasionally becoming slightly flushed with purplish-brown, rather gradually narrowed into the *beak*, which is c. 1 mm., slender, slightly compressed, smooth, with at the apex very small erect 'horns' and an inconspicuous notch. *Nut* not developed.

Wales. Merioneth (v.c. 48). A single plant on a wet rock just above the shore near Barmouth, National Grid reference 23/61, P. M. Benoit, 24.6.1954 in Herb. Kew. (2 stems) ; 1.7.1955 in Welsh Nat. Herb. (2 stems) and Herb. Sandwith (1 stem).

The hybrid, which is very similar to *C. binervis*, is compared in the following table with the parent species from the Barmouth district. The best distinguishing characters are in italics.

	<i>C. binervis</i>	Hybrid	<i>C. punctata</i>
Stem	Typically tall.	As in <i>C. binervis</i> .	Often shorter.
Male spike	1, often with a smaller one at base, distinctly pedunculate, <i>stout</i> (3.5-4 mm. thick), clavate, <i>dark brown to greyish-hoary</i> ; <i>remains of filaments present</i> .	1, occasionally with a smaller one at base, distinctly pedunculate, <i>rather stout</i> (2.5-3 mm. thick), ellipsoid-cylindric, <i>light brown</i> ; <i>remains of filaments absent</i> .	1, very shortly pedunculate, <i>very slender</i> (1.5-2 mm. thick), cylindric, <i>pale yellowish-brown</i> ; <i>remains of filaments present</i> .
Male glumes	Dark purplish, at least near the pale midrib.	\pm pale purplish near the pale or greenish midrib.	Pale yellowish; midrib green.
Stamens	<i>Exserted</i> ; <i>anthers dehiscent</i> .	<i>Included</i> ; <i>anthers indehiscent</i> .	<i>Exserted</i> ; <i>anthers dehiscent</i> .
Female spikes	Usually 3, very distant, especially below, \pm tapering downwards into the peduncle (a spike having its least spreading utricles at its base and often a few odd florets on the peduncle).	3, very distant, especially below, \pm tapering upwards and abruptly contracted into the peduncle (a spike having its most spreading utricles at or near its base and no odd florets on the peduncle).	3-4, the upper often not very distant, scarcely tapering, abruptly contracted into the peduncle, which has no odd florets.
Bracts	All falling far short of top of stem.	As in <i>C. binervis</i> .	At least the middle ones usually overtopping the stem.

	C. binervis	Hybrid	C. punctata
Female glumes	Very obtuse, dark purplish-brown.	Obtuse, <i>pale purplish-brown</i> .	Rather acute, <i>pale yellowish to colourless</i> .
Utricles	Spreading 40-70° when mature. 3.5-4 mm. long. Ovate, trigonous with sharp lateral angles, gradually narrowed into the beak. Soon becoming flushed with or entirely coloured purplish-black, rather shiny.	Spreading 50-70° when mature. 3.5-4 mm. long. Ovate, compressed-trigonous with very sharp lateral angles when fresh, flat when pressed, gradually narrowed into the beak. Occasionally becoming slightly flushed with purplish-brown, rather shiny.	Spreading <i>c.</i> 90° when mature. 3-3.5 mm. long. Roundish, obscurely trigonous to compressed-terete, rather abruptly narrowed into the beak. Becoming a uniform pale brown when mature, never flushed with purplish-brown, very shiny.
Beak	<i>Stout, much compressed, with conspicuous divergent 'horns' and notch.</i>	<i>As in C. punctata.</i>	Slender, slightly compressed, with small erect 'horns' and an inconspicuous notch.
Nut	<i>Normally developed.</i>	<i>Not developed.</i>	<i>Normally developed.</i>

I wish to thank Mr. E. Nelmes for his kind help in connection with the writing of this paper.

I. AN INLAND ARMERIA OVERLOOKED IN BRITAIN

Part 1

By E. J. GIBBONS and J. E. LOUSLEY

The aggregate species *Armeria maritima* (Mill.) Willd. has been the subject of considerable taxonomic research in Britain, and several workers have attempted to recognise segregates. For example, as early as 1849, Babington described four species in an elaborate account, but later work has made it clear that these, and other segregates brought to notice later, cannot be accepted, and that the group exhibits a range of variation which deserves study on modern lines. The variants so far described fall into two broad groups:—the first of maritime plants scattered round the coast; the second of inland montane plants. Both groups include several variants which may be ecads, or of higher grade, but it is not proposed to discuss these here—the purpose of this paper is to draw attention to an inland lowland segregate of which the significance in the British flora has been overlooked since the first discovery of the plants more than two centuries ago.

Since 1953, one of us (E.J.G.) has been much interested in an *Armeria* growing in the vicinity of Ancaster, South Lincolnshire, v.c. 53. In 1954, she sent a rooted plant to Dr. H. G. Baker, then of the University of Leeds, who is working on the group over a wider field. He provisionally determined it to be "*A. maritima* Willd. var. *elongata* Marsson" (nomenclature based on the treatment of the genus by Lawrence (1940).

In September, 1955, E.J.G., with Mr. and Mrs. R. C. L. Howitt, took J.E.L. to see a colony growing above an old sand-pit. These plants showed quite clearly that this identification is correct. The plant differs conspicuously from all other British material of *Armeria maritima* seen by us from coastal or mountain districts. With its long leaves and tall glabrous scapes bearing heads of flowers, the outer bracts of which are distinctly narrow, it is morphologically well separated from all of the segregates previously described from this country. It is well known, however, from sandy heaths in north central Europe. Specimens were exhibited at the B.S.B.I. Exhibition Meeting on November 26th, 1955, and the identification was confirmed by Dr. A. Melderis and others who have known it in central Europe.

The following description is based on material collected at Ancaster:—

Leaves 6—12 cm. long and 1—1.5 mm. broad, flat, not fleshy, with a single prominent nerve, usually fringed with scattered hairs on the margins. Scape glabrous, 20—55 cm. tall. Capitula $1\frac{1}{2}$ —2 cm. broad; outer bracts pointed, pale brown; corolla bright rose.

NOMENCLATURE

The name applied to the thrifts by Linnaeus was *Statice armeria*, and his description (1753) covers the plant with which we are particularly concerned here, as well as the coastal and other segregates. Lawrence (1940, 1947) has already pointed out that there is little doubt that the specimen of "*Statice armeria*" in the Linnean herbarium should be referred to the taxon now under discussion, and this is also true of the specimen in *Hortus Siccus Cliffortianus* which should be regarded as the type of his species.

A deliberate restriction of the name *Statice armeria* to the particular taxon now under

consideration was made by Pollich (1776), before Hoffmann (1800) described it as *Statice elongata* as follows:—

“*S. elongata*, scapo simpliciter elongato capitato glabro.

Fl. dan. t. 1092. In arenosis; fl. Jun.-Aug. (Folia in utraque linearia plana obtusa, in priori angustiora glabra, in hac latiora pubescentia.)”

The Ancaster specimens match the illustration in *Flora Danica* cited by Hoffmann.

The Linnean genus *Statice* included the sea-lavenders as well as the thrifts, and in 1809 Willdenow established the genus *Armeria* to describe the thrifts alone. This generic name was conserved by the International Botanical Congress in 1935, and is included in the list of *Nomina Generica Conservanda* issued as an appendix to the current Code of Botanical Nomenclature. The correct name, as a species, for the taxon which is the subject of this paper appears to be *A. elongata* (Hoffm.) Koch (1823).

As a variety the correct name is *A. maritima* var. *elongata* (Hoffm.) Crépin (1884). This greatly antedates the same combination made by Lawrence (1940), and Mansfeld (1941). Lawrence cited “*A. maritima* var. *elongata* Massart, *Fl. Neu Pom.*” which, by combining the name of one author with the title of the work of another, has caused confusion. Massart (1913) published “*Armeria maritima elongata*” but did not indicate the rank of the taxon and did not cite the basynym. If, on the other hand, Lawrence intended Marsson’s *Flora von Neu-Vorpommern* (1869), as some have supposed, the combination used in that work was *A. vulgaris* var. *elongata* (Hoffm.) and this combination had been published in 1826 by Mertens & Koch.

The main synonymy of the taxon under consideration is as follows:—

Statice armeria L. (1753) *Sp. pl.*, 1, 274, *pro parte*.

Statice armeria L. sensu Pollich (1776) *Hist. Pl. Palat. Elect.*, 1, 318.

Statice elongata Hoffm. (1800) *Deutsch. Fl.*, 1800, 1, 150.

Statice armeria var. *elongata* (Hoffm.) DC. (1805) *Fl. Franc.*, ed. 3, 3, 419.

Armeria vulgaris Willd. (1809) *Enum. Pl. Berol.*, 333.

Armeria elongata (Hoffm.) Koch (1823) *Flora*, 6, 698.

Armeria vulgaris var. *elongata* (Hoffm.) Koch (1826) in Mert. & Koch, *Deutsch. Fl.*, 2, 487.

Armeria campestris var. *hoffmannii* Wallr. (1842) *Beiträge*, 1, 204.

Armeria maritima subsp. *elongata* (Hoffm.) Bonnier (1927) *Fl. Complète*, 9, 54.

This plant has been the subject of considerable confusion in European floras of the 19th century but recent works (e.g. Hegi, 1927) have given clear accounts. The distribution is centred on the sandy heaths of the north German plain, where it is common, and it extends east to White Russia (Smolensk), south to the Danube, and west to the Saar and Palatinate on the eastern boundary of France (fig. 1). The distribution is thus of a continental type, in contrast to that of restricted *A. maritima*, which is an Atlantic type extending eastwards along the northern coast of Europe. *A. elongata* sometimes grows in the vicinity of the coast although, apart from its apparent edaphic requirement of an easily draining soil (well provided by “sand fields” near the coast), its ecological requirements do not restrict it to the coast, and most of its stations are inland. This will be discussed further later in this paper. Individuals intermediate in their morphological characters sometimes occur and may be found in populations which are in general uniform. It therefore seems unlikely that the rank of species, which has been accorded to the taxon under discussion, is justified, but since it exhibits clear morphological, ecological and geographical differentiation, the appropriate grade is that of subspecies, and we propose to treat it accordingly. This view is supported by the experimental work carried out by Professor Baker (see Part 2).



Fig. 1. Distribution of *Armeria maritima* subsp. *elongata*. Based on Hegi, *Fl. Mitt.-Eur.*, 5/3, 1890 fig. 2885.

In this grade the correct name, to which Mr. J. E. Dandy has kindly drawn our attention, appears to be *A. maritima* subsp. *elongata* (Hoffm.) Bonnier (1927). It is of interest that Bonnier knew it only, in the area covered by his *Flora*, from calamine soils in Belgium, the same habitat as given by Crépin and Massart.

RECORDS OF AN INLAND ARMERIA IN EASTERN ENGLAND TO 1955

An inland *Armeria* from Lincolnshire was first recorded by Vincent Bacon in 1726 and, as will be seen from the list of records given below, it has been observed at intervals up to the present time. It is remarkable that most recent botanists have either ignored the records, or else dismissed them as errors, in spite of the respectability of the recorders and the availability of supporting evidence which could have been found with little difficulty. Horwood's views, published in 1933, are worth citing as an example of the attitude which led to this plant's being ignored for so long. He wrote "This can only be a mistake. Inland stations for Thrift are all montane. These localities (Saltby, Grantham, Sleaford, Belvoir Castle) are at low elevations c.400 ft. It is an error without doubt."

The detailed records which follow are set out under the approximate dates to which they refer. The localities are marked on the map in figure 2.

- 1726. Near Grantham. Bacon (1726, and see also Woodruffe-Peacock, 1898).
- 1749 "abundantly about Sleaford and Grantham, Lincolnshire." Pulteney (1749).
- c.1752. "This I never saw spontaneously growing in Leicestershire but observed it abundantly upon the heaths about Sleaford and Grantham in Lincolnshire." Pulteney (1752).
- 1757. "This is not only found in the marshes near the sea, but farther in the inland parts of the country, as I observed in Lincolnshire, where it is very plentiful about Grantham and Sleaford. I have not seen it nearer Leicester than upon a heath not far from Belvoir Castle." Pulteney (1757, 826).
- c.1763. Grantham. Martyn (1763, 63).

1780. "circa Easton prope Grantham." Sibthorp ex Druce (1910). The records and herbarium in the University Department of Botany, Oxford, have been searched by Mrs. H. N. Clokie but she has been unable to trace a specimen or the list cited by Druce.
1789. "In meadows; about Grantham and Sleaford, and upon a heath not far from Belvoir Castle." Pulteney ex Gough (1789 & 1806).
- c.1795. Lincoln Heath—specimen in Herb. Banks (Herb. Mus. Brit.).
1795. "On a heath near Saltby but more plentifully on the chalk plains near Grantham and Sleaford, Lincolnshire." Pulteney ex Nichols (1795).
1855. Wilsford and Ancaster. Lowe (1856).
1884. Grantham. E. E. Browne ex Peacock MS (1922).
1895. Manthorpe, Grantham. S. C. Stow in Herb. Lincoln.
1896. "Leaving Grantham . . . the party proceeded . . . along the Manthorpe Road. In an adjacent field, Thrift (*Armeria maritima*) was observed growing in plenty . . . Mr. Cordeaux, who noticed the plant in several other localities, was of the opinion that it is a relic of the time when the tide had access to the valley, being perhaps the only surviving representative of the old fitty-flora." Goulding (1896).

The unlikelihood of this historical interpretation is shown not only by the taxonomic nature of the thrift material, but also by the complete absence of other maritime species.

1930. Near Oarcliff (sic) spring, Wilsford. H. Fisher in Herb. Fisher, Nottingham.

From 1932 to 1935 Mr. Edward E. Orchard of Ancaster was familiar with an *Armeria* growing in several fields near his home, and in 1953 showed it to E.J.G. and Mr. Roger Hull. In 1954 E.J.G. showed the plant to Mr. and Mrs. R. C. L. Howitt, who found a new locality by the railway east of Ancaster.

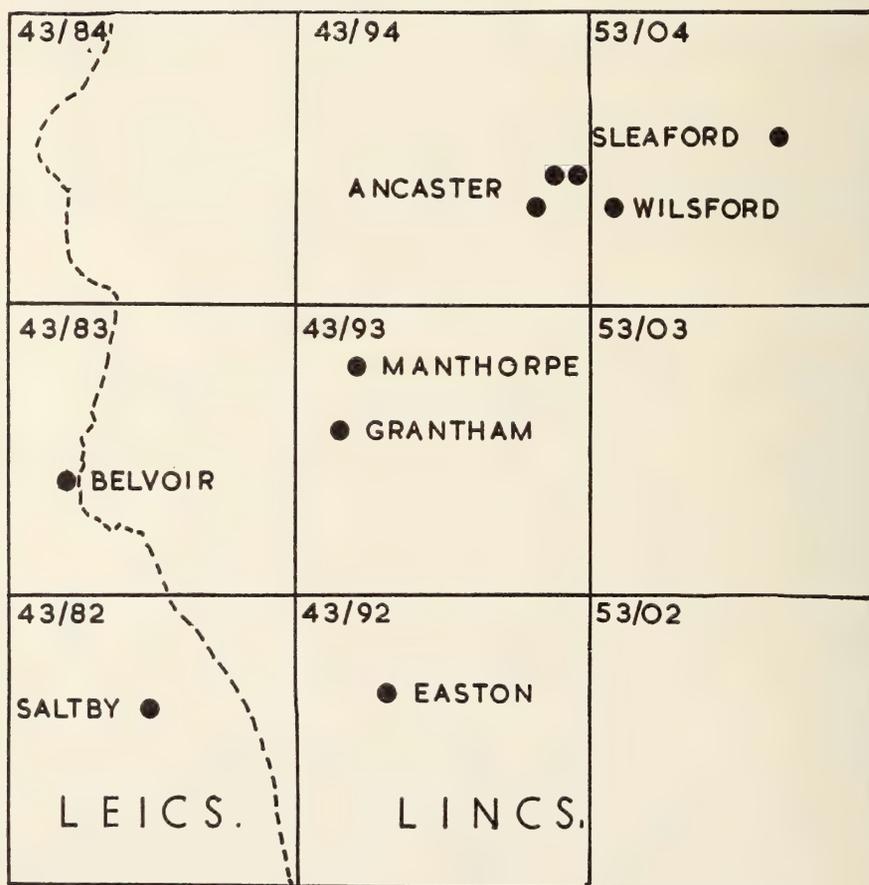


Fig. 2. Distribution of an inland *Armeria* in Leicestershire and Lincolnshire as recorded 1726 - 1955 plotted on the 10-kilometre squares of the National Grid.

The localities recorded up to 1955 thus extend from Saltby and Easton in the south to Belvoir, Grantham and Manthorpe, and north-east to Ancaster, Wilsford and Sleaford (Fig. 2). They occurred in the following 10-kilometre squares of the National Grid :— 43/82, 43/83, 43/92, 43/93, 43/94, and 53/04. The distance between the extreme recorded localities is about 18 miles, and distances of the various stations from the nearest coast vary from 18 to about 33 miles. The heath near Saltby is in Leicestershire (v.c. 55), as was probably the heath near Belvoir Castle which is near the county boundary; all the remaining localities are in South Lincolnshire. The habitats were described as heaths, fields and meadows.

The area over which the records extend was part of the old Lincoln Heath, which in the 18th century was open "heath," without hedges and with few landmarks. Most of it was calcareous grassland which was destroyed by enclosure and the plough, and now survives only in a few small patches of old turf by roadsides or quarries. The term "heath" was applied in its general sense to connote open uncultivated land and there is no reason to suppose that it implied the presence of species of Ericaceae or acid soils. Pulteney's records show that an *Armeria* was abundant about Grantham and Sleaford "on the chalk plains" and that he knew it in other widely scattered places on this part of Lincoln Heath. Since his time enclosure has destroyed most of the stations. It is now known to persist only near Ancaster and Wilsford in the habitats discussed later in this paper.

PRESENT DISTRIBUTION

During the summer of 1956 an attempt was made to examine the old localities and ascertain the present distribution. The results are as follows :—

V.c. 55, Leicestershire. Belvoir Castle and Saltby Heath were visited by J.E.L. and Mr. and Mrs. R. C. L. Howitt on July 7th. Near the former no suitable ground was found, and remnants of Saltby Heath were searched without success. Here there are remnants of rough limestone grassland with abundant calcicoles which are likely to be representative of the Heath before it was broken up by agriculture. The last Leicestershire record for *Armeria* dates from 1795, and it seems unlikely that it still persists.

V.c. 53, South Lincolnshire.

A. Easton. A very brief examination of this district on July 7th showed that it is intensively cultivated and no suitable ground was seen from public roads. The parkland of Easton Hall should be investigated.

B. Grantham and Manthorpe. Mr. L. Bond of Grantham has made enquiries and states (*in litt.*) that friends remember it about Manthorpe, that most of the land is now built over and he has searched in vain.

C. Ancaster—Wilsford. *Armeria maritima* subsp. *elongata* is still plentiful over a considerable area. The habitats are discussed below :—

PRESENT STATIONS IN THE ANCASTER-WILSFORD DISTRICT

Armeria maritima subsp. *elongata* was seen by us in the following 11 stations (Fig. 3) on July 9th, 1957 :—

(1) Ancaster. Pasture, west of the school and north of the stream. Here the *Armeria* is restricted to calcareous grassland on sandy soil (pH 7.1) on the drier upper slopes, and is absent from the lower damper, rushy parts of the field. The pasture is heavily grazed by cows. For associated species see Table 1.

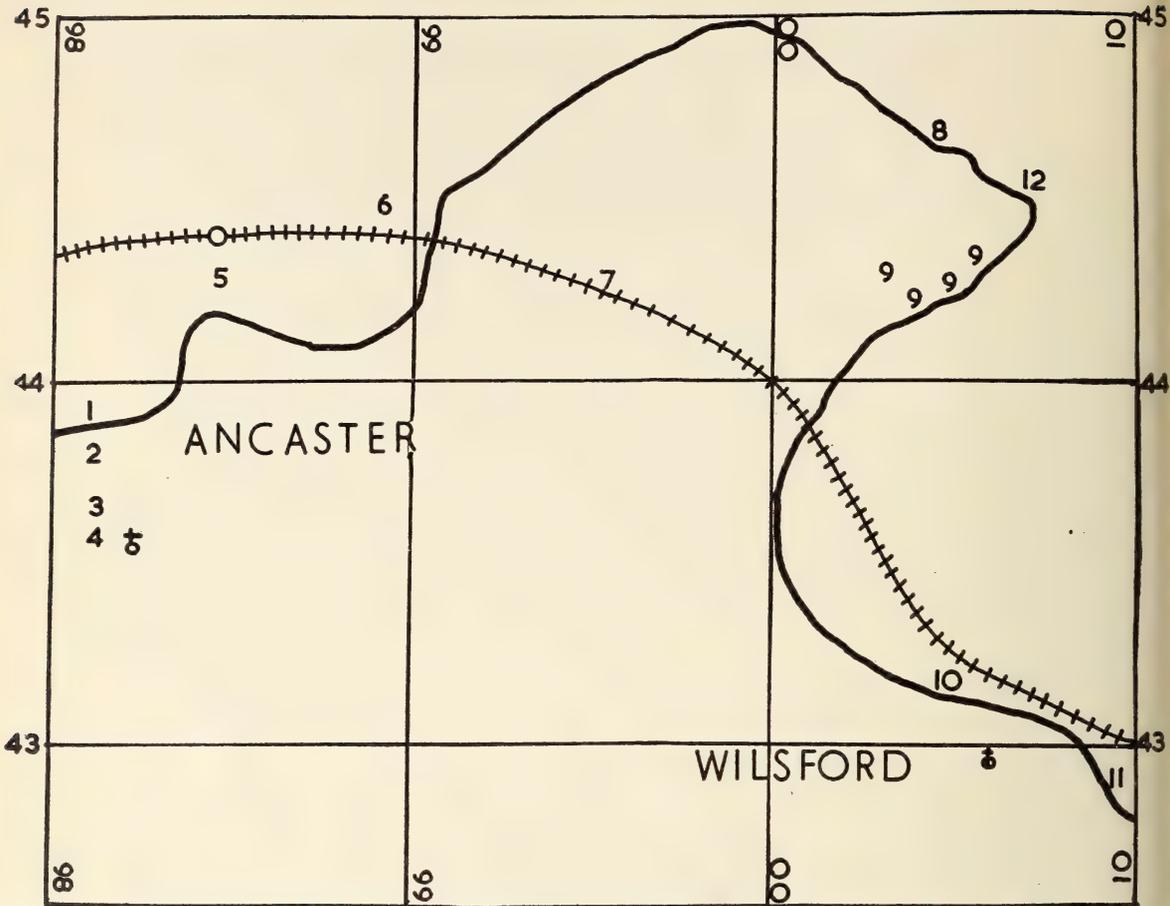


Fig. 3. Habitats of *Armeria maritima* subsp. *elongata* about Ancaster and Wilsford, S. Lincolnshire, examined in 1956, showing their relationship to the stream and the railway. The numbers refer to the habitats discussed in the text, and are plotted on the 1-kilometre squares of the National Grid.

(2) Ancaster. Pasture south of (1) and separated from it by a stream. Vegetation very similar to (1).

(3) Ancaster. Burial ground, immediately south of (1), and west of the church. This burial ground is calcareous grassland which has been fenced off from the adjoining pastures for at least 30 years. Only part is occupied by graves but the whole is scythed periodically. At the time of our July visit, the area within the fence was a glorious sheet of pink from the thrift which was in full flower, in marked contrast to the pastures outside, where flowers were scarce. This abundant flowering was repeated six weeks later after the grass had been cut. From the distribution of thrift on neglected graves it seems likely to have arisen on these from self-sown seed rather than to have been planted. For associated species see Table 1.

(4) Ancaster. Pasture adjoining the burial ground to the south. A heavily grazed pasture, drier than (1) and (2), and thrift less plentiful. Calcareous grassland, with similar associated species including *Carduus nutans* and *Plantago media*.

(5) Ancaster. Pasture sloping south from railway station to the stream. As in (1), no *Armeria* was found in the lower, damper part of the field, but it was abundant on the drier upper slopes towards the railway station, where the vegetation was that of calcareous grassland (see Table 1). The soil is sandy with pH 8–8.3.

TABLE 1.

Species associated with Armeria maritima subsp. elongata at four localities at Ancaster, July 9th, 1956.*

Locality	1 Pasture	3 Burial ground	5 Pasture	6 Sandpit
pH	7.1	—	8 — 8.3	8 — 8.3
<i>Achillea millefolium</i>		o		
<i>Agrostis tenuis</i>	f			a
<i>Armeria maritima subsp. elongata</i>	f	d	a	r
<i>Arrhenatherum elatius</i>		f	o	
<i>Bellis perennis</i>	f			
* <i>Brachypodium pinnatum</i>				l
<i>Briza media</i>	o	o		
<i>Carex flacca</i>	l			
<i>Centaurea scabiosa</i>		o		
* <i>Cerastium arvense</i>	o			
<i>Chrysanthemum leucanthemum</i>		o		
* <i>Cirsium palustre</i>	l			
<i>Cynosurus cristatus</i>	f			
<i>Dactylis glomerata</i>	o			o
<i>Festuca ovina</i>	o	c		
<i>F. rubra</i>		o		
<i>Filipendula vulgaris</i>	r			
<i>Galium verum</i>	o	a		
<i>Helictotrichon pubescens</i>				f
<i>Hieracium pilosella</i>		r		
<i>Holcus lanatus</i>	o	f	c	o
<i>Hypochoeris radicata</i>				r
<i>Knautia arvensis</i>		r		
<i>Koeleria gracilis</i>		a		o
<i>Leontodon hispidus</i>	a			
<i>Lotus corniculatus</i>	o		f	
<i>Poa pratensis</i>				a
<i>Phleum nodosum</i>	o		o	o
<i>Plantago lanceolata</i>	f	o		f
<i>P. media</i>	a	a	c	f
<i>Poterium sanguisorba</i>	o		o	
<i>Primula veris</i>	l			
<i>Prunella vulgaris</i>	o			
<i>Ranunculus acris</i>	o	f		
<i>R. repens</i>	f	o		
* <i>Rhinanthus minor</i>	o			
<i>Rumex acetosa</i>	l	f		f
* <i>Senecio jacobaea</i>	f			
* <i>Taraxacum officinale (agg.)</i>	o			
<i>Trifolium dubium</i>	o	f		
<i>T. repens</i>	o		f	
<i>Trisetum flavescens</i>	f	f	a	o
* <i>Urtica dioica</i>				l
<i>Vicia angustifolia</i>				o
<i>V. hirsuta</i>		c		f
<i>V. sativa</i>		r		o

* The species marked with an asterisk were added from the lists made by Dr. Baker when he visited the same colonies with E.J.G. on August 10, 1956.

(6) Ancaster. Rough grassland above an old sand-pit, north of the railway. Here the *Armeria* is rare, and hidden in tall grass (Plate 10). The soil is sandy, pH 8—8.3, with associated species (see Table 1) mainly characteristic of calcareous grassland. The differences between this habitat and those described above appear to be attributable to the absence of grazing. This was the locality from which material was collected in 1955. Mr. Orchard tells us that it formerly grew in quantity in two fields east of the sandpit which are now ploughed.

(7) Limestone grassland above railway cutting between Ancaster and Wilsford. One plant was seen about $\frac{1}{2}$ mile east of (6) in a narrow strip of grassland by the top of the cutting through Lincolnshire Limestone (oolite) rock, growing in a very shallow soil over the limestone.

(8) By stream 1 mile north of Wilsford village. Thrift was seen in quantity, associated with *Carduus nutans*, on the top of a sandy bank on the north side of the stream.

(9) On west bank of stream $\frac{1}{2}$ mile N.E. of Waterloo Farm, Wilsford. This is Fisher's 1930 Norcliff (= Oarcliff) Spring locality, or very near it. On the bank of the stream the *Armeria* is plentiful in sandy but wet ground, and exceptionally fine. The associated species included:—*Arrhenatherum elatius*, *Cerastium arvense*, *Cirsium arvense*, *Equisetum fluviatile*, *Galium verum*, *Glechoma hederacea*, *Linum catharticum*, *Dactylorhiza fuchsii*, *Potentilla anserina*, and *Reseda lutea*.

Above the stream, and sloping up towards the west, is a seeded meadow in which sheep were grazing. In this, thrift was scarce in a mixture of sown grasses in which *Lolium perenne* was dominant, and *Anthoxanthum odoratum*, *Bromus mollis*, *Dactylis glomerata*, and *Rumex acetosella* common. From information obtained later by E.J.G. it seems likely that this field was ploughed in 1955, which accords with the crop. The *Armeria* here is a relic of a former pasture, which it is said to have coloured "pink all over."

(10) Wilsford. Pasture between village and main-road. *Armeria* is confined to a band on the drier upper slopes in calcareous grassland with *Plantago media* abundant. This field was more thoroughly examined by E.J.G. and Dr. Baker on August 10th and it was found that the thrift was restricted to the higher parts of the pasture (thereby avoiding the coarsest grass), and associated with *Cirsium acaulon*, *Thymus drucei*, and *Torilis nodosa*. The field was very closely grazed by sheep. Some thrift plants here were up to 65 cms. in diameter and revealed their considerable age by decayed centres.

(11) Wilsford. Pasture above stream on east side of the village.

The following station was also examined by E.J.G. and differs considerably from the others:—

(12) Rough pasture, on the east side of the stream, about 1 mile north of Wilsford village. This is on the opposite bank of the stream from (9), and slightly north of it. Only two plants of *Armeria* were seen in what appears to be original grassland. The associated species included:—*Agrostis tenuis*, *Calluna vulgaris*, *Campanula rotundifolia*, *Leontodon leysleri*, *Ononis repens*, *Rumex acetosella*, *R. tenuifolius*, *Scleranthus annuus*, *Ulex europaeus*.

DISCUSSION OF THE STATIONS

The stations in which the plant was seen in 1956 show a fairly close relationship to the stream which flows through Ancaster and Wilsford. With the exception of (7) which is on Lincolnshire limestone, they are probably all in places marked as Post-glacial River Gravels or Alluvium on the latest (c.1885) one inch geological drift map. These River Gravels extend west of Ancaster and then swing south through Manthorpe

PLATE 10.



Armeria maritima subsp. *elongata* in rough grassland above an old sand-pit, Ancaster (habitat 6, p.—).
September, 1955.



to Grantham. It is therefore likely that the statement by Woodruffe-Peacock (1922) that the Grantham and Manthorpe localities were on "Modern River Gravels" was correct.

From a comparison of the twelve stations in which *Armeria maritima* subsp. *elongata* was seen in England in 1956, it seems that its ecological requirements are as follows:—

(A) Good drainage. In fields sloping up from wet to dry areas (1, 2, 5) it was evident that the thrift avoided the wetter parts. This preference for well drained stations was confirmed by its abundance in the dry soil of the burial ground (3), and occurrences elsewhere. The apparent contradiction of one habitat on the bank of the stream (9), with a mixture of plants characteristic of wet and dry places, is not difficult to explain. The root systems of *Equisetum fluviatile* and other species with higher water requirements were at a much lower level than those of the thrift.

(B) Absence of competition from taller vegetation. In the places where the *Armeria* was most plentiful, competing vegetation was kept down by grazing (stations 1, 2, 4, 5, 9, 10, 11) or scything (3). Where the grass was rank (stations 6, 7) the plant was scarce. The tall habit develops in places where there is no higher vegetation (e.g. 26 cm. in habitat 5; 47 cm. in station 9), as well as where the plant is competing with tall grasses (47 cm. in September in station 6).

(C) Soil reaction. In the three meadows where the soil was tested the pH ranged from about 7.1 to 8.3, and the associated species were more or less characteristic of limestone grassland. The other stations all appear to have basic soils, with the probable exception of 12, where the associated species indicate acid conditions.

Abroad, the habitats of *A. maritima* subsp. *elongata* vary considerably ecologically. According to Hegi (1927), the plant is most characteristic of "Calluna- and *Sarothamnus*-heath and poor meadows with *Festuca rubra*, *Agropyron repens*, *Koeleria cristata*, *Brachypodium pinnatum*, *Pimpinella saxifraga*, *Achillea millefolium*, etc.". It also grows on grass-heath of several types, and on serpentine. The associated species listed by Hegi include several which are calcicoles in this country. According to Massart (1913) it is one of four species restricted to calamine soils in Belgium. The known English habitats are well within the range of those described from abroad. They have much in common with the sandy fields and gravelly hillslopes on which the plant grows in southern Sweden, and offer a marked contrast to the habitats of the atlantic subsp. *maritima*. The populations examined show general uniformity in the characteristics of smooth and tall scapes, rather flat heads with long sheaths and elongate outer bracts, and the long flat leaves. This also applies to the few old specimens seen from the Lincoln Heath area, and it is reasonable to assume that all the records cited refer to the same subspecies.

The distribution of the old records and Pulteney's statement that thrift was plentiful on the "chalk plains" (by which he intended limestone—the nearest chalk being farther east) are consistent with the association of the plant with soils with a high base content. Until the enclosure of Lincoln Heath such places would probably have been grazed by sheep and the plant thus protected from the competition of tall grasses. Peacock (1922) wrote "Horses and goats eat it, but not sheep, or it would have been exterminated long ago inland. I have seen it inland and on the shore where sheep were grazing, but it was quite untouched by them. In pasture where horses were grazing it was eaten. Here by a goat, too." Our observations do not entirely support those of Peacock, since it seems that sheep will eat it quite readily. Grazing operates to the advantage of thrift, however, by removing the competition for light. The parish of Ancaster was not enclosed until 1770 and the greater part of it was then "a wild and barren heath" (White, 1842, 666),

but no doubt flocks of sheep were grazed there, as elsewhere in Lincolnshire where vast numbers were kept. It seems likely that the present stations, and those destroyed by enclosure, were available for *Armeria maritima* subsp. *elongata* for a very long period.

SUMMARY

An inland *Armeria* has been known to grow in Lincolnshire since 1726 and in adjoining parts of Leicestershire since a little later. The old records are reviewed, and twelve stations where the plant was studied in 1956 are described and discussed. It is shown that this non-maritime *Armeria* is distinguishable from *A. maritima* (Mill.) Willd. subsp. *maritima* on morphological, geographical and ecological characteristics and it is therefore best treated as a subspecies, *A. maritima* subsp. *elongata* (Hoffm.) Bonnier based on *Statice elongata* Hoffmann.

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Part 2

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During the course of an extensive series of cultivation – and breeding – experiments on the species and races of *Armeria* which I have carried out in the experimental gardens of the University of Leeds and the Carnegie Institution of Washington (at Stanford, California), material of coastal and montane forms of *A. maritima* as well as the grassland thrift here called subsp. *elongata* has been studied. These studies, which have enabled certain biosystematic conclusions to be drawn as well as making more certain the identification of plants from nature, will be published elsewhere.

The South Lincolnshire populations described here were visited by me whilst on leave from the Gold Coast, on August 10th, 1956, under the guidance of Miss Gibbons. Leaf- and scape-samples were collected and some ecological observations were made. The latter were in close accord with those reported by Miss Gibbons and Mr. Lousley. This visit enabled me to confirm my previous provisional determination of the plants as *A. maritima* “var. *elongata*,” for they agree in key characters with those in culture from Scandinavian and Polish sources. In particular, they have long, glabrous scapes bearing rather flat heads of pale flowers. The outermost bracts of the heads are rather long and pointed while the involucre sheath is also long (up to 2.5 cm.). The pilosity of the calyces is pleurotrichous. The leaves have a single prominent nerve and are deeply channelled on the upper surface; in a majority of plants they are ciliate on their margins.

The treatment of these grassland thrifts suggested by Miss Gibbons and Mr. Lousley as a subspecies of *Armeria maritima* distinct from the coastal and montane forms is in agreement with the results obtained from the experimental production and breeding of hybrids in Leeds and follows the treatment given to other ecological races in this species by me (Baker, 1953). Such hybrids between subsp. *elongata* on the one hand and British coastal material on the other have proved fully fertile in the first and second generations (Baker, 1954a, and unpub.). The chromosome-number of subsp. *elongata* has been determined both from the Continental cultures and from Ancaster and shows $2n = 14$, the same as for the other subspecies of *A. maritima*.

The South Lincolnshire populations, like material of subsp. *elongata* from all sources, show the pollen- and stigma-dimorphism (Baker, 1948a, b, 1954 a, b) characteristic of the Old World, non-arctic species of the genus. Dimorphism of this type in a population is an indication that cross-pollination is the general rule and that isolated plants are unlikely to produce viable seed.

It was clear from the burial-ground population in August, 1956, that the thrift was very much more abundant on relatively new graves where there was little shading and root-competition by grasses than it was in places where the grasses had become rank. This is in agreement with observations made in the garden at Leeds where this taxon, like the other subspecies of *Armeria maritima*, has shown itself very unfavourably affected by artificial shading which, in particular, reduces flowering considerably. The length of the leaves of the Ancaster plants could be related directly to the rankness of the grass around them (cf. Table I).

A similar picture was provided in the pasture (Habitat No. 1). Here the thrift was particularly frequent on the ant-hills. Although both the grasses and the leaves and scapes

TABLE 1.

	Mean leaf length (cms)	Standard error	Mean leaf breadth (cms)	Standard error	Mean Leaf Index (length/ breadth)	Standard error
Ancaster: pasture heavily grazed by cattle. Habitat No. 1	6.0	± 1.4	0.11	± 0.03	61.3	± 23.3
Ancaster: portion of Burial Ground unoccupied by graves (scythed occassionally). Habitat No. 3	7.1	± 1.8	0.11	± 0.03	67.3	± 20.9
Ancaster: sandpit; in long grass Habitat No. 6 (one plant)	20.4	—	0.10	—	204	—

of the thrift were freely grazed by cows and the flowering of the latter was seriously reduced thereby, its very existence must have been favoured by the complete removal of shading. This sensitivity to grass-competition must be kept in mind when considering the history of subsp. *elongata* in Britain.

The sub-fossil record of *Armeria* in the British Isles is a relatively complete one, including Inter-glacial, Full-glacial and particularly Late-glacial finds. Unquestionably, *Armeria maritima* was widespread over the country at all elevations during Late-glacial time when a relatively open, unwooded vegetation prevailed (Baker, 1948 *b*, 1956; Godwin 1956). With the subsequent increase of grass-competition and the development of forests, the thrifts were eliminated except from the mountains and at the coasts where shading from trees and tall grasses did not apply. A similar history may be cited for *Plantago maritima* and *Silene maritima*, the frequent associates of the thrifts on sea-coast and mountain.

A comparable picture has emerged from studies of sub-fossil deposits from the continent of Europe (cf. Iversen, 1940; Szafer, 1945; Jessen, 1949). Nevertheless, there is no reason to believe that the hardy thrifts which kept so close to the ice included subsp. *elongata*; indeed, in cultivation at Leeds, this subspecies has revealed itself rather susceptible to harm from frosts. Its more or less continuous, unicentric distribution in north-central Europe, covering much once-glaciated land, suggests that its range has largely been achieved post-glacially even if its origin is older. Iversen (1940) concluded that *elongata* is a very young race deriving either from coastal or alpine (var. *alpina* Lawr.) material. However, the extent of its distribution shows that its history is not a short one even though it may be a *relatively* young subspecies.

None of the 34 stations for fossil and sub-fossil *Armeria* in the British Isles listed by Godwin (1956) seems particularly likely to have harboured subsp. *elongata*, for those of less than Late-glacial age are all montane or coastal. Consequently, we are left with only the historical record dating from the early eighteenth century and a suspicion that the subspecies was never widespread in Britain. On the other hand, there is no more reason than with the Breckland "Continental" species (which have much in common with subsp. *elongata*) to suppose that the establishment of the subspecies in Britain was not entirely natural (cf. Pigott and Walters, 1954, p.102).

This is not to deny the importance of man's influence upon the present abundance of the subspecies. Clearly it is favoured by grass-cutting in the Ancaster burial-ground (and, presumably, in any hay-field) and by the grazing of domestic animals in the pastures,

while the forest-clearing which began in eastern England in the Neolithic Age may even have prevented its extermination long ago. One wonders how it may have fared before man became a farmer but suspects that it reached its heyday in a bygone predominantly pastoral period. At present the increasing disturbance of the ground by ploughing and building is undoubtedly reducing its numbers considerably.

It is possible that there is evidence of a less direct nature suggesting the aboriginal status of subsp. *elongata* in eastern England. Amongst other features, this subspecies is characterised by ciliate margins to its leaves, a feature which has not varied in cultures from four Scandinavian and Polish sources. Nevertheless, the analysis of leaf-samples from Ancaster No. 1 and No. 3 populations showed 48% and 28% of glabrous leaves, respectively. The glabrous leaves showed no significant differences in length or breadth from those with ciliate margins but both samples were uniformly slightly narrower and less obviously flattened than is usual in the subspecies (1–1.5 mm. against up to 3 mm.). Narrow, glabrous leaves are particularly characteristic of salt-marsh forms of *Armeria maritima* and are also found in a considerable proportion of the rock and shingle populations.

In British coastal and montane populations of *Armeria maritima* the scape is characteristically hairy (unlike the glabrous condition in subsp. *elongata*). Glabrous scapes have not been noticed in large numbers of herbarium specimens which have been seen, nor have they appeared in cultures derived from British sources with the exception of Blakeney Point and Scolt Head Island (Norfolk) where the proportion of plants with glabrous scapes may rise as high as 40% in some samples. No cultures have been raised from seed collected on the Lincolnshire coast, but this should be tackled by someone residing conveniently near who might also pay attention to the shape of the outermost bracts of the plants (for they are short and blunt in typical coastal plants but long and pointed in subsp. *elongata*). Subsp. *elongata* bears paler flowers and begins to produce them later in the season than is usual in chasmophytic plants from the coast but any observations upon these features will be complicated by the great variability of the latter and by the similarity of salt-marsh plants to subsp. *elongata* in these characters.

Too much must not be made of these aberrant characters in eastern English populations for, in both cases described here, the peculiarities could have had their origins in mutations within the races concerned and owe nothing to mutual introgression. Nevertheless, if the area occupied by *elongata* were sufficiently larger in the past, the races could well have come into contact and hybridised, for we know that they are interfertile and outbreeding. The only other detailed reports of such a re-assortment of characters between *elongata* and the coastal forms (Turesson, 1922) have referred to populations of unquestionably mixed ancestry on the southern Swedish coasts. Such taxonomic treatments as those of Christiansen (1931, 1932) show that it is in regions where the ranges of the forms overlap, particularly around the Baltic coastline, that intermediate plants of all sorts may be found (which he called var. *intermedia* and credited with four forms and sub-forms). Focke (1903) had earlier grouped the hybrid populations from the German Baltic coast as *Armeria ambifaria*.

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HYPERICUM CANADENSE L. IN WESTERN IRELAND

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DISCOVERY

The recent discovery of *Hypericum canadense* L. in the west of Ireland adds a new member of the 'North American element' to the flora of the British Isles. I have described elsewhere (Webb, 1957) the history of its discovery, and it can be very briefly summarised here.

In July, 1954, while looking for another plant on the west shore of Lough Mask, I saw a plant of what I took to be *Hypericum humifusum*, but with an unusual suberect habit. I took it into cultivation and kept it under observation for two years, but on account of over-dry conditions of culture it did not thrive and, beyond suspecting that it was not a normal specimen of a recognised British species, I could not identify it. I decided therefore to revisit the station in 1956, and on August 12th, in very wet weather which did not permit extensive observations, rediscovered the plant in some abundance and readily identified it as *H. canadense* on my return to Dublin next day. I visited the station once more in early September and made some observations on the plant's distribution and habitat.

Meanwhile I had learnt that Mr. D. McClintock had visited the station on August 14th, had found the plant, and had independently identified it as *H. canadense*. I had told him of the mysterious *Hypericum* and indicated the locality when he had passed through Dublin ten days earlier: at that time my plans were uncertain on account of illness, and we were therefore unable to co-ordinate our visits.

DESCRIPTION

The following description is compiled from Irish material. In a few minor particulars it differs slightly from the descriptions in American Floras; but it is clear in any case that the species is rather variable.

A slender, erect, entirely glabrous herb, more or less tinged with deep purplish red, especially in the lower parts, (3-) 12-20 cm. high, usually with the appearance of an annual and probably for the most part behaving as such, but capable in some circumstances of perennating by buds at ground level. Stem slender but stiff, sharply 4-angled and often slightly winged, usually unbranched except in the inflorescence, but in the strongest plants bearing a few short erecto-patent branches from the lower axils. Lower leaves elliptical or broadly oblong, $6-8 \times 2.5-3$ mm., patent; middle and upper ones narrow-oblong or linear-oblong, $12-20 \times 2-4$ mm., nearly erect; all plane, entire, obtuse, sessile and semi-amplexicaul, usually 3-veined and with numerous pellucid glands. Flowers up to 30 or more, but often only 3-9, in a regular dichotomous cyme; lowest bracts resembling the leaves, upper ones very small and narrow. Sepals 4 mm. long, ovate-lanceolate, obtuse or subacute, marked with pale or reddish streaks which represent lines of tissue similar to that which forms the pellucid dots on the leaves. Petals $3-4 \times 1.5-2$ mm., elliptical to narrowly obovate, deep golden yellow, usually with a crimson line on the back, rather widely separated, giving the flower a somewhat stellate form. Stamens 13-25,

PLATE 11.



Hypericum canadense L. at Gortmore, Lough Mask, Co. Mayo, forming a conspicuous dark fringe to the streamlet which runs through the sandy flat. In the middle distance is the former shore-line with miniature dunes; beyond this the road, and beyond it, to the right, part of a drumlin.

rather obscurely grouped into five bundles. Ovary conical, with three short, spreading styles. Capsule deep red, ovoid-conical, 5-6 mm. long, somewhat exceeding the persistent calyx. Seeds straw-coloured, oblong, 0.5 mm. long.

In natural conditions the flowers open only in bright weather. In pot culture they remain closed even in bright light if the atmosphere is dry; they may be induced to open by covering the plant with a bell-glass.

The Irish plant appears to come rather closer to the variety *magninsulare* Weatherby (1928) than to the type. This variety, described from Grand Manan Island, New Brunswick, is distinguished by petals which are narrower and more pointed than in the type, and have a red line on the back. In the Irish plant the red line is present; the shape is intermediate between the two extremes figured by Weatherby.

STATION AND HABITAT

The main station, in which the plant is very abundant, as may be seen from Plate 11, is on a wet sandy flat in the townland of Gortmore, which lies on the west shore of Lough Mask near the south end, about half a mile north of the entrance of the Owenbrin River. The grid reference (on the provisional grid used for Ireland in the Distribution Maps Scheme) is 94/1336. The station is now in Co. Mayo, but as it was in Co. Galway till 1898 it should be regarded as falling in v.c. H.16 (W. Galway). Smaller colonies can be found near the main one for about half a mile in either direction; and one small outlier has been located over 6 miles to the north-east, at the north-west corner of the lough. This latter falls in v.c. H.27.

The distribution of the plant in its main station makes it clear that it is most at home in very wet conditions and that it requires a peaty, or at least a base-poor soil. Boggy flushes in the grassy vegetation of the sand-flat, pools in adjoining areas of shallow bog, the sides of drains cut in peaty soil, the edges of streamlets too small to cut for themselves a permanent, grass-free bed – these are the situations in which *Hypericum canadense* flourishes and is most abundant. The drainage comes from a hillside that is entirely composed of acid rocks, so that the general facies of most of the surrounding vegetation is calcifuge and peat is plentiful. The opposite shore of Lough Mask is, however, entirely limestone, and the water in the lake is consequently alkaline (pH about 8.0). In the lower part of the flood-zone, therefore, the vegetation is less calcifuge, and base-demanding plants like *Samolus valerandi* become frequent. But at this point *Hypericum canadense* stops short; I did not see it growing close to the lake-water, nor in immediate juxtaposition to *Samolus*.

The species most constantly associated with *Hypericum canadense* are *Hypericum elodes*, *Anagallis tenella*, *Juncus acutiflorus*, *J. kochii*, *Carex panicea*, *C. demissa*, *Molinia caerulea*, *Eleocharis multicaulis*, *Ranunculus flammula* and *Hydrocotyle vulgaris*.

GEOGRAPHICAL DISTRIBUTION

Hypericum canadense is found over a wide area of eastern North America, northwards to Newfoundland, southwards to Alabama, and westwards to Manitoba and Iowa. It has been recorded from two other stations in Europe: on the gravelly shores of peaty lakelets near Servance (Hte.-Saône) on the western flank of the Vosges (Bouchard, 1954), and on a heath near Almelo in eastern Holland (Jonker, 1935). In the former it was, curiously enough, discovered in the same year as I first noticed it in Ireland, but the Dutch station has been known since 1934.

HISTORY

Three hypotheses can be entertained with some degree of plausibility :—

1. The plant has recently been introduced to Ireland by human agency.
2. It has recently arrived in Ireland by natural means.
3. It is an old-established native.

1. This seems on the whole the least probable. Human operations in the neighbourhood of Gortmore are confined to small-scale farming and football. The district is wild and remote : five miles, in a direct line, from a village and fifteen miles from a port. The road carries little traffic, most of it local. The only American import ever likely to reach the district is maize or other grain, and this does not provide a likely medium for the transport of the seeds of a bog-plant. Indeed, it is difficult to cite an example of a bog-plant that is distributed by ordinary human operations of commerce or transport; and *Hypericum canadense* would scarcely be cultivated in a garden by even the most assiduous collector of novelties.

Bouchard believes that the only possible means of its arrival in France by human agency was by American troops in 1917-8, and does not regard this explanation as probable.

It should perhaps be mentioned here that *Hypericum majus*, a closely related American species, but sometimes favouring drier ground and more likely to behave as a ruderal, has recently been found on the Bohemian boundary of Bavaria (Merxmüller & Vollrath, 1956). *H. mutilum*, also native of America, is naturalised in northern Italy.

2. The only natural means of dispersal that suggests itself is transport on the feet of birds. No bird migrates regularly across the North Atlantic, but occasional stragglers of about a dozen American species find their way to Ireland now and then. The Greenland white-fronted goose, which has been rather freely invoked by botanists in recent years, breeds in west Greenland and winters either in North America or in Ireland. It cannot be seriously considered as a means of transport until *Hypericum canadense* has been recorded for west Greenland.

In general, this hypothesis, though it cannot be ruled out, seems rather a last resort and has no positive evidence for it.

3. The geographical range of *Hypericum canadense* agrees well enough with that of half a dozen other species which are generally (though not universally) believed to be relict in Europe for it to be reasonable enough to entertain the hypothesis that it is not a recent arrival in Ireland. There are, however, four questions to be answered before this interpretation can be accepted.

(i) Could the plant have withstood the last glaciation, and perhaps earlier glaciations as well, in western Ireland? We do not know enough to give a confident reply, but a plant that grows in central Newfoundland today cannot be exactly tender, and seems at least as likely to survive as *Najas flexilis*, which we know on fossil evidence has done so.

(ii) Is an annual (and *Hypericum canadense* may be regarded virtually as such) likely to persist in abundance as a relict in a restricted area? The *a priori* answer is No; if it can seed itself well enough to persist in abundance it should be able to spread if suitable habitats are near at hand. On the other hand *Helianthemum guttatum*, an annual which is clearly relict everywhere in the British Isles, has one mainland station (Three Castles Head, Co. Cork) where it grows in fair abundance in a very restricted area despite the close proximity of much similar terrain.

(iii) How do recent changes in the level of Lough Mask affect the issue? The cutting of the abortive Corrib-Mask canal about a century ago lowered the level of Lough

Mask, and if it could be shown that the ground on which *Hypericum canadense* now grows had been under water till then, this would tell strongly against the relict hypothesis. An examination of the 1841 Ordnance map shows, however, that this is not so. The strip of ground exposed varies in width, in this part of the shore, from 80 to 300 yards, and, save for a few tongues which follow the course of streams, *Hypericum canadense* stops short of the lake-shore by just about this distance.

The issue is complicated by the fact that there is an obvious earlier shore-line higher up (referred to by Praeger in *The Botanist in Ireland*), and the *Hypericum* grows mainly, though not entirely, below the level of this. As to its age, however, we have no clue; granted that it must be post-glacial, it may well be old enough for the plant to have been able to adjust itself at its leisure to the change in water-level by migrating downwards for a hundred yards or so.

(iv) Why had it not been seen before, and is its simultaneous discovery in Ireland and France simply a coincidence? Here is the real crux. The plant is so abundant and (thanks to its dark red foliage) conspicuous that I still find it impossible to understand how I noticed only a few plants in 1954, and how Praeger failed to notice it twenty years earlier when he visited the spot. The earlier visits were at the beginning of July, when the plant is presumably much less conspicuous, but this argument alone does not convince. Bouchard also poses the first part of the question, for his French station is close to a lake well worked by local botanists. He points out, however, that *Littorella uniflora*, an abundant and constant associate of *Hypericum canadense*, had not hitherto been recorded from the department of Haute-Saône. It is clear that the botanists had followed a well-worn trail with their noses to the ground. This was seldom Praeger's practice, but even as keen-eyed a botanist as he can fail to see one plant when he is looking for another, and on this visit he was looking for *Lycopodium inundatum*. It is perhaps revealing that he did not record the presence of *Pilularia*, a very rare plant in Ireland, which here grows in some abundance, very close to the *Hypericum*. In Holland, although the plant was not recognised till 1934, it was collected as long ago as 1909 (specimen in herbarium of Royal Netherlands Botanical Society) and it is remarkable that here, too, it grows accompanied by a rare plant (*Wahlenbergia hederacea*: only station in Holland) which was discovered here only a year before the *Hypericum*. In all cases, therefore, there is evidence that the locality had not been well searched by botanists.

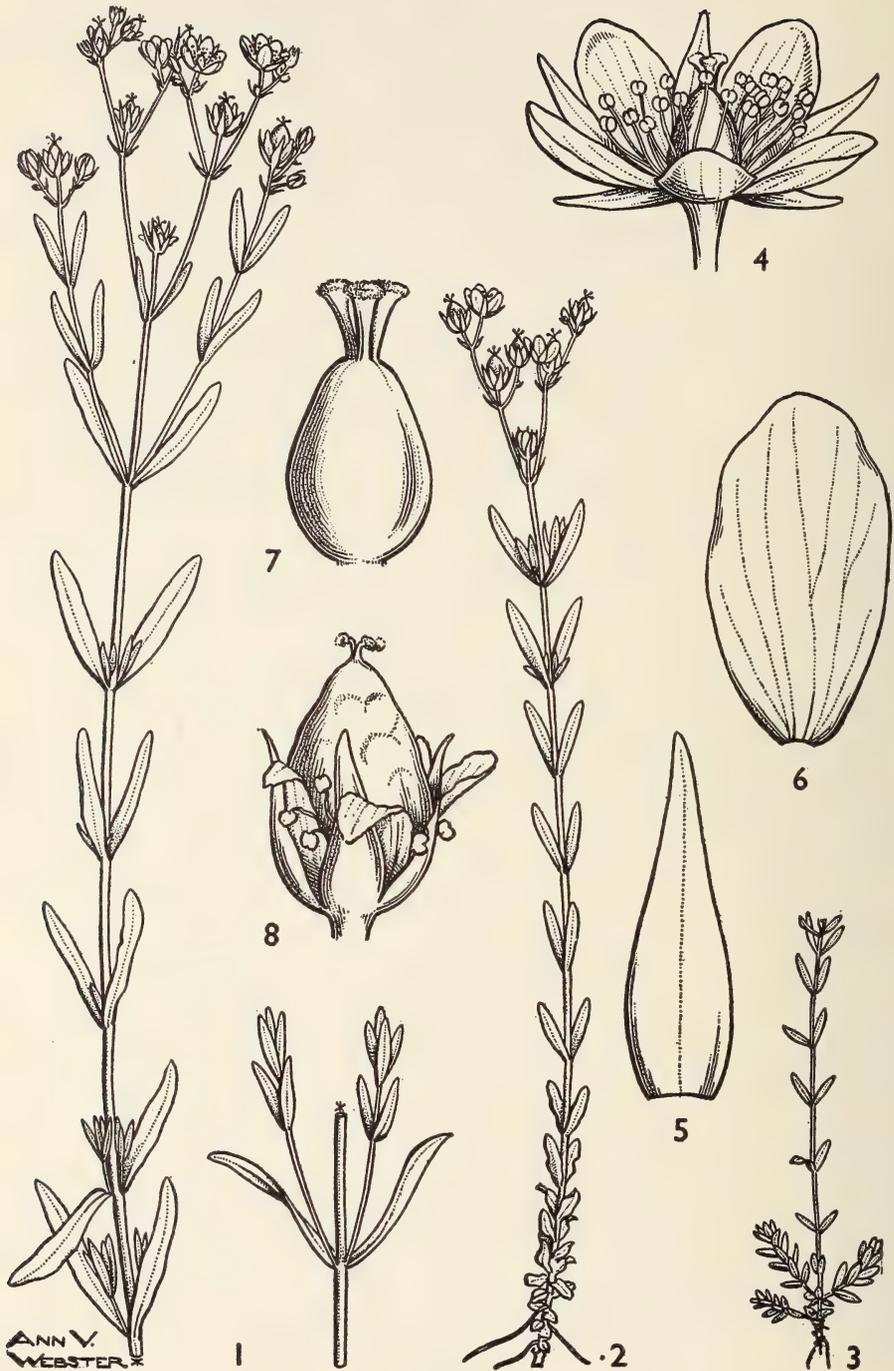
It will be seen that in my opinion the balance of evidence is in favour of supposing that *Hypericum canadense* is relict in Ireland and on the Continent. The coincidence of its simultaneous discovery in Ireland and France is remarkable, but it may be recalled that *Erica mackaiana* was discovered in the same year in Ireland and in Spain. And what possible chain of circumstances could have led to the transport of seeds from America to Lough Mask, to a Dutch heath and to the Vosges, without having scattered them broadcast all over Western Europe?

The answer should however, be provided by the next few years. If the plant spreads rapidly, then it is almost certainly a recent introduction by one means or other, if it shows no sign of spreading, it is only reasonable to accept it as an old-established native.

I am indebted to Mr. J. E. Lousley, Mr. N. Y. Sandwith and Dr. N. K. B. Robson for the references to occurrences of *H. canadense* and related species on the Continent.

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Hypericum canadense L. from Gortmore. 1. Large plant. 2. Average-sized plant. 3. Plant after six weeks' greenhouse culture, showing perennating shoots at ground level. 4. Flower. 5. Sepal. 6. Petal. 7. Gynoecium. 8. Nearly mature capsule. 1-3, natural size; 4 and 8, $\times 6$; 5-7, $\times 12$.

NOTE

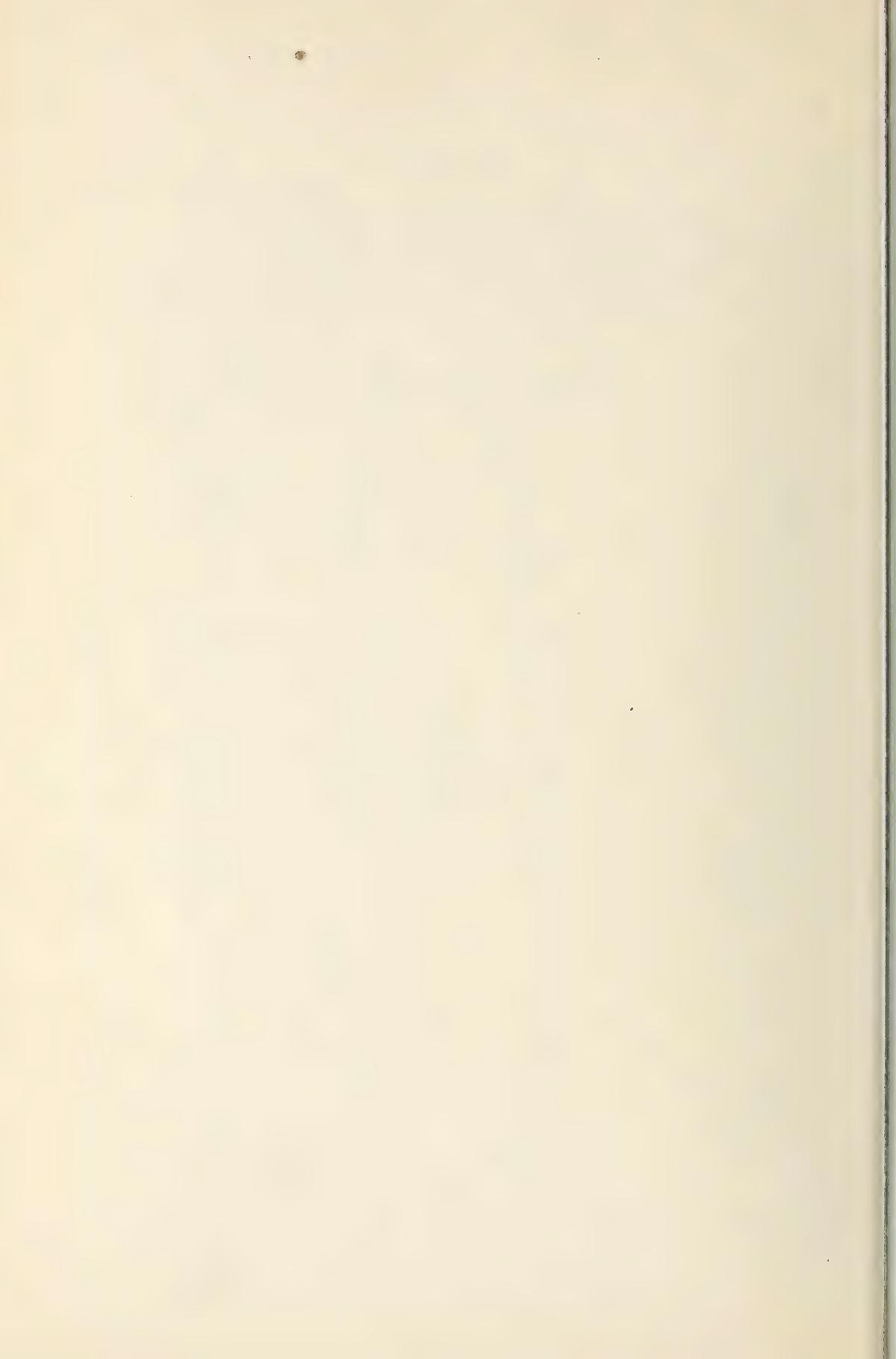
By D. McCLINTOCK

When on 4 August 1956 in Dublin, Prof. Webb showed me the *Hypericum* which was puzzling him, it reminded me most, and still does, of small *H. linarifolium* Vahl. At L. Mask on August 14th with my sons Andrew and Hugh, ignorant of his having been there two days earlier, I found the plant in plenty (which I hadn't expected), apparently at the extreme N end of its main area, since I could see neither the *Lycopodium* nor the *Pilularia*. Some 170 species growing within 100 yards or so of the plants (including arable, a small quarry and hedges) were entered on a mapping card. I specially looked out for other species of *Hypericum* and listed *H. androsaemum* L., *H. pulchrum* L., *H. tetrapterum* Fr. and *H. elodes* L., but not *H. humifusum* L. It is not common in Ireland, but the ground was in parts not unsuitable for it.

H. canadense L. (whose name and importance I naturally only discovered on my returning home and to my Gray) was in open associations, some in swampy mud but mostly in wet sand. No doubt this wetness was due to the plant's preference rather than to Hobson's choice in a record wet August, but in pot culture at home in Kent so far (Feb., during an admittedly wet winter) it has been happy enough without abnormal watering.

The plants when picked came up very readily by their shallow roots. For this reason I sent back nearly all I collected to be planted; the remainder are in Herb. Lousley. Three months later twelve of these had produced winter buds while eight had died - some very possibly because of damage in collection or transit. This proportion, two out of three, is supported by Fernald who describes it as "perennial by short leafy off-shoots" rather than by Britton and Brown who say it is annual. But this particular result may have been effected by the stimulus of transplanting and the point can only be settled by a visit to Co. Mayo in mid-winter and actually seeing what happens in nature in Ireland.

The pot with the twelve growing specimens was shown at the Exhibition meeting of the Society at S. Kensington on 24 Nov. 1956 together with the seeds from the plants which had not over-wintered, herbarium sheets of Irish and American material, the mapping card and brief notes. The seeds and half the growing plants have been sent to the Botanic Garden at Cambridge.



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BIOLOGICAL STUDIES IN *POA ANGUSTIFOLIA*

By D. M. BARLING

Royal Agricultural College, Cirencester

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INTRODUCTION

The agronomic importance of *Poa pratensis* in north-west Europe and North America has stimulated its intensive study, and that of the genus *Poa* as a whole (Nygren, 1954 for references). The latter is now known to contain apomictic and sexual species, which frequently hybridise to give intermediate types, and the considerable taxonomic interest of this generic complex has been discussed by Gustafsson (1947), Stebbins (1950), Nygren (1954) and Melderis (1955). *P. pratensis* itself contains obligate and facultative apomictic forms (Tinney, 1940, Åkerberg, 1942), and the situation, as well as the complexity found within single plants, has been neatly described by Nygren (1951). The species is thus a polymorphic group with a wide range of chromosome numbers that form an aneuploid series, and is classified into sub-species, form-complexes or part populations by various workers (Nannfeldt, 1935, Åkerberg, 1942; Tutin, 1952; Gustafsson, 1947; Hylander, 1953); or separated into distinct species (Lindman, 1926; Hultén, 1950; Hubbard, 1954). The subspecies recognised in Sweden are subsp. *pratensis*, subsp. *angustifolia* (L.) Lindb. fil., subsp. *irrigata* (Lindm.) Lindb. fil. (including *P. subcaerulea* Sm.), and subsp. *alpigena* (Fr.) Hiit. According to Åkerberg (1942), they are linked by intermediate forms particularly where they overlap. The first three taxa are distributed in the British Isles. The more recent work at the Carnegie Institution (Clausen *et al.*, 1947-53) has emphasised the extreme complexity of *P. pratensis*, as well as its capacity to hybridise with other *Poae* and produce intermediate forms. This American work has thrown considerable light on the taxonomy of *P. pratensis* and resulted in several agronomically useful strains.

The present work is an attempt to study the autecology and taxonomy of *P. angustifolia*, chiefly in the Cotswold area, though observations on other areas have been made. A description of British *P. angustifolia* is given by Hubbard (1954). Åkerberg (1942) has made detailed studies of one Scandinavian strain and three plants intermediate with *P.*

pratensis; he gives chromosome numbers of 50-65, and demonstrates the presence of apomictic and sexual reproduction in wild plants.

It is thus apparent that the taxonomic opinions on *P. pratensis* are extremely complex, resolving themselves firstly into those of workers who consider it to be extremely polymorphic with four main subspecies grouped around focal types, and linked by intermediate forms, and secondly, those of workers who hold these subspecies to be sufficiently distinct to merit specific rank. In the present field-studies, populations have been found where *P. pratensis* is represented not only by the *P. angustifolia* complex, but where other shorter-culmed and broader-leaved forms* are present, and transplant studies have revealed phenological as well as morphological differences between them. It was thus important in sampling to select only those plants with narrow leaf-blades as typical of the *P. angustifolia* complex, and some of the reasons for this will be discussed later. It is intended to deal with the study of the more complex populations containing *P. angustifolia* and other forms of *P. pratensis* in a later paper.

DISTRIBUTION AND SYNECOLOGY

Hubbard (1954) states that the British distribution of *P. angustifolia* was incompletely known but that it was commoner in the south than in the north, and he also suggests (1948) that it should be common in Gloucestershire. Hultén (1950) gives the distribution in north-west Europe, showing it as common in southern Sweden and Norway, and also to the east of the Baltic and in Denmark. An approximate northern limit is given and it is noted that the species is found in dry lowland areas, but that the distribution is incompletely recorded. The species is classified as "Boreal-circumpolar lacking large gaps in its area." Active recording has been made by me since 1947, and a large number of stations have been recorded in Gloucestershire and neighbouring areas, and a well-scattered selection of these is given in Table 1., whilst four records are listed by Hubbard (1948).

Records are most common from three habitats: firstly from permanent grasslands, particularly rough swards; secondly from road verges and thirdly from the unploughed headlands of arable areas. The permanent grasslands of the Gloucestershire Oolites may be divided into two broad groups, the rough and the cultivated swards; *P. angustifolia* is usually present in the former, where *Brachypodium pinnatum* and *Bromus erectus* are sward dominants and the sward is rather open, with agricultural activities negligible. The cultivated grasslands are intensively grazed and mown, and may be dominated by *Lolium perenne* or *Festuca rubra*, and whilst *P. pratensis sensu lato* is very common, *P. angustifolia* is rare, being found in those which are continuously put to hay and where species such as *Helictotrichon pubescens* and *Bromus erectus* are common. Detailed observations of the rough areas, however, have revealed forms of *P. pratensis*, so that sympatric populations of *P. pratensis* and *P. angustifolia* are found. *P. pratensis* is also very common in trampled areas such as gateways (Bates, 1938), so that it is frequent at the entry to rough areas and on pathways through them; thus the two taxa may be brought together in this way. In the Cotswold area, road-verges are often wide and frequently dominated by *Bromus erectus* and *Brachypodium pinnatum*, and *P. angustifolia* is common. However, close trampling or mowing of verges may result in colonisation by *P. pratensis* and often in establishment of sympatric populations.

The unploughed headlands of fields are often narrow strips of old permanent pasture in which the species discussed above are common. One striking example of this was found near Little Hinton, Wilts., where a large stretch of downland had been wire-fenced into

*These forms have short culms, both glumes 3-nerved and pointed, usually single tillers per node under field conditions, and broad leaves on sterile tillers with hairs at the collar; they are therefore very similar to *P. subcaerulea*.

separate fields, and arable crops grown, so that the original grassland was found near the fences, and there *P. angustifolia* was common.

Thus it is clear that a study of *P. angustifolia* is bound to take considerable account of *P. pratensis* as a whole, for, apart from the critical taxonomic nature of the group, there is considerable sympatric distribution of forms in the Cotswold area. This association may amount to physical contact between tillers and rhizomes.

TABLE 1.

POA ANGUSTIFOLIA. Records in the Botanical Districts and vice-counties of Gloucestershire.

v.c. 33.	{	1. Broadway Hill. Chipping Campden
	{	2a. —
	{	2b.(north). Upton St. Leonards.
	{	2b. (south).
	{	3. Churcham.
v.c. 34.	{	4. —
	{	5. Didmarton. Pennsylvania. Cold Ashton.
	{	6. (south). Avening. Amberley. Minchinhampton. Frampton Mansell
	{	6. (north). Brimpsfield. Bisley. Camp. Chalford. Cranham. Edgeworth. Painswick. Tunley. Sapperton. Miserden.
v.c. 33.	{	7a. Aston Blank. Bourton-on-the-Water. Cleeve Hill. Great Barrington. Hampnett. Hazleton. Little Rissington. Sherborne. Stow-on-the-Wold. Turkdean.
	{	7b. Ampney Crucis. Birdlip. Cowley. Chedworth. Colesbourne. Duntisbourne Abbots. Elkstone. Aldsworth. Barnsley. Bibury. Fosse Bridge. Fosse Cross. Rodmarton. Tetbury. Bagendon. Coln St. Aldwyn. Quenington. Nr. Coln Rogers. Wistley Hill.

Records in adjoining vice-Counties.

- v.c. 6. Swainswick, nr. Bath.
 v.c. 7. Kemble. Fox Hill, Little Hinton.
 v.c. 23. Burford. Fullbrook. Chadlington. Hill Barn. Milton-under-Wychwood. Shipton-under-Wychwood.
 v.c. 36. Ross-on-Wye. Tretire. Weston-under-Penyard.
-

PHENOLOGY

The seasonal development of established plants under field conditions is described below, and amounts, essentially, to the development of fertile tillers with broad leaves very early in the spring, followed by growth of sterile tillers with narrow leaves, and eventually the production of rhizomes and new roots. This culminates in the emergence and seed production of inflorescences, followed by negligible growth. The striking features of this development are, first, the early development of fertile tillers, and secondly, the later development of essentially vegetative growth, particularly rhizomes and roots. The differences of leaf-width may lead to difficulties in identification during the spring, and particularly so when the winter kill of autumn leaves is complete, though the emergence of the sterile tillers soon resolves this difficulty.

SEASONAL STAGES OF DEVELOPMENT IN *P. angustifolia*.

Stage 1. Winter period : remains of culms visible with foliage severely damaged by frosts; plants difficult to find after prolonged severe weather; only youngest leaves may be green and are surrounded by dead leaves. Inflorescence primordia found with difficulty.

Stage 2. Late February – early March : plants tufted; new growth on surviving tillers of the previous year consisting of broad short leaves; inflorescence primordia differentiated; basal axillary buds on the fertile tillers commencing to elongate.

Stage 3. Mid-March to early April : tufted, more densely tillered; tillering intra-vaginal, fertile tillers elongating and robust with broad leaf-blades; tillers from basal buds leafy with long, narrow, leaf-blades; panicles well developed inside the fertile tillers.

Stage 4. Mid-April to early May : panicles emerging and in some localities emerged; leaves of fertile tillers beginning to die back; basal sterile tillers now with very long and narrow leaf-blades; extra-vaginal tillers developing into rhizomes that are white and fleshy, or into short tillers that further increase the diameter of the tufts; length of rhizomes variable and up to 30 cm.; old brown roots being supplemented by the new adventitious roots from base of tillers; overall appearance tufted. Some tufts without fertile tillers are probably the products of the previous years rhizomes. Many culms dead owing to insect attack and straw coloured.

Stage 5. May to July : panicles fully emerged with some late ones emerging; anthesis, seed-setting and seed-ripening all occurring; tall culms with their broad leaf blades and often short flag-leaf, contrasted with the well developed sterile tillers with long narrow leaf-blades; shorter leaf-blades at base of the sterile tillers now withered; ripe seeds being shed in mid-July. Tips of rhizomes tillered but small. Many sterile tillers dead or withering.

Stage 6. August and autumn : all fertile tillers dead; seed more or less completely shed; sterile tillers now the main part of the plant; lower leaves dead; plants tufted often still connected by slender rhizomes, new small tufts establishing. Some tillering under less competitive conditions. Growth during August affected by rainfall.

Inflorescence primordia are found in January and very easily found in early March, and details of fertile tiller development are listed below with approximate dates.

Stage	Date and notes
1. Inflorescence primordia	December – January
2. Elongation of tiller	Commences 20th March
3. Spikelet primordia	Commences 12th March
4. Panicle emergence	Earliest 15th April
5. Meiosis in anthers	1st May
6. Pollen grains	15th May
7. Panicle branches open	26th May onwards
8. Anthesis	1st June onwards
9. Seed setting and ripening	23rd June onwards
10. Seed shedding	9th July onwards

Several workers have demonstrated the importance of photoperiod and low temperature on flowering responses in grasses (Evans, 1927; Cooper, 1951). In *P. pratensis*, Peterson and Loomis (1949) in their studies on North American material demonstrated that autumn conditions of low temperature and short day length are necessary for inflorescence initiation in the species, though they also point out that the same conditions are repeated in the early spring. In a comprehensive account of *P. pratensis* (Evans, 1949)

refers to this latter work and states that only autumn-formed tillers become fertile, and records much data on the phenology of *P. pratensis* in America, with correlations between photoperiod, temperature and seasonal development. At Cirencester the differentiation of inflorescence primordia in *P. angustifolia* was easily found in early spring, in late January both outdoors and in the greenhouse, and also in December, but with greater difficulty. Dissection of apical buds during early March showed varying degrees of bud differentiation within and between plants. The emergence of panicles was accelerated under greenhouse conditions of higher temperature (Table 2). Field emergence also varied from centre to centre in the Cotswolds, being earliest in sheltered areas with a southerly aspect, and so, presumably, being a temperature response. One of the most striking features of 1955 and 1956 was the fact that emergence of *P. angustifolia* preceeded that of all other perennial grasses in the area of study, though the subsequent floral development was slow and far behind later-heading, but essentially early, species such as *Alopecurus pratensis*.

TABLE 2.
Panicle emergence in some greenhouse transplants.

Source	Date of emergence in greenhouse	Date of emergence in open
Deer Park 1.	4. 3.	3 to 9. 4.
Deer Park 2.	3. 5.	10. 5.
Deer Park 3.	4. 5.	10 to 14. 5.
Deer Park 4.	10. 4. to 4. 5.	21. 4. to 14. 5.

PLANT CHARACTERS

Populations. As an auxiliary to more detailed studies with a phenological bias, it was decided to sample several populations to compare morphological characters, for the populations as such are the effective breeding units, and are subjected to actual selection pressure so that they are the important sources of variability. Five areas were studied in the Cotswolds and one near Duddington in Northamptonshire, all centres overlying Oolitic Limestone formations. A single plant-unit was taken as a tuft of tillers clearly separated from any other by a distinct rhizome of a prior season. Considerable morphological variability was encountered in the populations, and as forms were frequently found that resembled poorly developed plants of the *P. pratensis* type, care was taken to collect only those with distinctly narrow leaf-blades on the sterile tillers as typical of the complex.

The data presented in Table 3 illustrate the variability within populations and also between areas. In all cases the number of fertile tillers was low, being highest in a more fertile enclosed and cultivated area near Cirencester.

Although the appearance of the inflorescence is similar, detailed data of length and branches from the basal node vary considerably, as do culm-height, and leaf-blade measurements. The differences between sterile leaf-blades and flag leaf-blades are increased by the fact that the former tend to lengthen with the advancing season, and the latter lengthen then shorten with the advancement of the culm. It is probable that the increasing photoperiod is associated with the former and panicle-competition for nutrients with the latter. Rhizome production was sporadic, and varied considerably from sample to sample, so that it is possible that intra- and inter-plant competition may have a profound influence, as was, in fact, found by transplant studies (Table 4). The study of competition in other Gramineae (Donald, 1954 ; Thomas, 1956) has shown that vegetative and reproductive capacities are affected. Hairiness was recorded from the upper leaf-blade surface on the sterile tillers and all plants were found to be hairy on this basis.

TABLE 3.
Population data on the morphology of *P. angustifolia*.

Centre and Sward Type	No. sterile Tillers	No. fertile Tillers	No. New Rhizomes	Length of Panicle mm.	Height of Culm mm.	No. Branches at lowest panicle node	Flag Leaf mm.		Sterile Leaf mm.		% Hairiness
							Width	Length	Width	Length	
Deer Park <i>Festuca rubra</i> - <i>Bromus erectus</i>	6.45 ± 0.43	1.65 ± 0.15	0.65 ± 0.10	81.40 ± 2.75	398.04 ± 4.08	3.72 ± 0.11	2.42	36.35	1.55	225.1	100
Royal Agricultural College <i>Bromus erectus</i>	6.95 ± 0.63	1.80 ± 0.27	0.80 ± 0.14	102.40 ± 3.01	575.70 ± 25.10	4.14 ± 0.19	3.12	44.50	1.69	200.2	100
Two Mile Lodge <i>Brachypodium pinnatum</i>	3.64 ± 0.36	1.32 ± 0.16	0.88 ± 0.16	88.45 ± 3.36	546.60 ± 13.23	3.81 ± 0.14	2.58	29.66	1.50	147.0	100
V.W.H. Kennels <i>F. rubra-Lolium perenne</i>	8.45 ± 1.00	2.85 ± 0.46	1.35 ± 0.20	113.05 ± 2.81	584.00 ± 14.60	3.94 ± 0.15	3.13	43.32	1.64	258.0	100
Three Mile Bottom <i>Bromus erectus</i>	4.70 ± 0.45	1.10 ± 0.07	0.40 ± 0.21	81.20 ± 4.08	531.10 ± 17.67	3.80 ± 0.01	2.43	31.00	1.34	172.4	100
Duddington Nr. Stamford <i>Bromus erectus</i>	4.85 ± 0.47	1.30 ± 0.18	1.35 ± 0.27	80.25 ± 3.29	428.60 ± 12.40	4.25 ± 0.17	2.58	36.60	1.68	193.8	100

As many data of phenological interest were found, the details are considered below for the different parts of the plants.

Population densities vary considerably and only one centre (Deer Park) has been recorded because of its unusually high count of 2.4 tufts per sq. foot.

TABLE 4. *Morphological characters of wild and transplanted individuals from Deer Park.*

Type	No. fertile tillers	No. sterile tillers	No. of rhizomes	Ht. of culms	Secondary fertile tillers	Length inflorescence	Branches lowest node
Wild	1.65	6.45	0.65	398.04	2.0%	81.40	3.72
(1956)	± 0.15	± 0.43	± 0.15	± 4.88		± 2.75	± 0.11
Transplants	6.40	20.40	3.00	588.70	33%	100.00	4.44
(1956)	± 0.11	± 1.90	± 0.50	± 8.50		± 3.21	± 0.12

Tiller and Root Development. There are three tiller types to be found in the complex, namely the sterile and fertile tillers and the rhizome. The sterile tillers are actively formed during the spring by the tillering of the fertile shoot, and these new tillers augment those that overwinter on the weaker of the previous season's rhizomes, and are later further augmented by the tillering of the rhizomes developed later in the spring. These sterile tillers can be readily recognised by their narrow leaf-blades and fine appearance. The longevity of these sterile tillers varies; some, produced in the spring of one year, flower and eventually die in the following season, thus persisting for up to fifteen months. Some sterile tillers may be killed before their first winter by insect or animal attack and so have an intermediate existence, often being found dead in late May. Where conditions are poor, some of the tillers do not develop inflorescence primordia and so may persist a little longer and usually do not flower before their death, others may produce late inflorescences. Tillers weakly developed at the apices of rhizomes often, under competitive conditions, survive from June of one year to the end of the following season in a sterile condition and exceptionally may gain overwinter.

The development of the fertile tiller from the sterile condition involves a complete change in the length and width of the leaf-blade; this is also accompanied by a slightly greater width of the tiller.

Rhizomes are produced by extra-vaginal tillering either during or just after the emergence of the panicles, and so can easily be found in May. The rhizomes are white and fleshy in appearance, with the scale-leaves a little longer than the internodes, and are of varying length. In some cases they are exceptionally short and later, after the death of the subtending leaf, appear like any other tiller in the tuft, often forming a second tuft up against the original one; in transplants they may be up to 40 cm. long, but are somewhat shorter under field conditions. The rhizomes root at the node and may branch from axillary buds, but are of the determinate type as described by Oakley & Evans (1921). The older rhizomes are harder and brown in colour with variable internode-length and diameter (Table 5).

A study of root development in *P. pratensis* by Sprague (1933) found considerable seasonal differences. New roots were formed in the spring, amounting to half of the roots being regenerated, and a decrease in root-weight occurred at the period of heavy tillering and stem-growth, being followed by a gradual recovery when tiller-growth was less.

TABLE 5.
Rhizome Measurements at Different Centres.

Centre	Internode Length (mm.)	Diameter (mm.)
Deer Park	9.68 ± 0.67	1.003 ± 0.0497
Duddington	9.10 ± 0.904	0.780 ± 0.0427

New roots are first found in *P. angustifolia* during the spring period, the first being found in late April, they become abundant in May, and usually appear just before the rhizomes. During the season as a whole they are but few in number and not of the prolific nature found in such species as *Lolium perenne*. Thus, until these appear, the old roots of the previous development are responsible for absorption during the period of elongation of the fertile tillers and the production of sterile tillers, and are probably functional for several seasons. Thus, in general, there is a distinct lag in development of vegetative as opposed to fertile tillers in *P. angustifolia*, and it thus differs from that found in the *P. pratensis*-complex.

Leaves: The sterile tillers of *P. angustifolia* have narrow but long leaf-blades, and this is one of the outstanding taxonomic features of the complex; the longest measured are as follows:—

SOURCE	WIDTH	LENGTH	RATIO
Duddington	1.95	560	1 : 287.18
Three Mile Bottom	1.80	522	1 : 290.00
Trent Lodge	1.60	418	1 : 261.25
Jackaments Bottom	1.80	481	1 : 267.22

However, the successive leaves of the sterile tillers differ in length and width, and similar differences are found in the fertile tillers (Table 6). During this work, a ratio of leaf-width to length was calculated, the width being measured microscopically just above the ligule, and the length to the nearest millimeter.

TABLE 6.
Leaf Blade measurements from fertile and sterile Tillers of *P. angustifolia* (mm.)

Centre	Fertile Tiller								Sterile Tiller				
	Old Leaves		New Leaves						Leaves				
	1	2	1	2	3	4	5	6	1	2	3	4	5
(A) Width	1.6	1.6	1.4	1.9	3.0	4.2	3.9	—	1.2	1.5	1.5	1.8	1.8
Length	—	350	65	67	116	149	101	—	60	140	141	168	266
Ratio	—	218.7	46.4	35.3	38.7	35.5	25.9	—	50.0	93.3	94.0	93.3	147.8
(B) Width	1.64	1.6	3.08	3.28	3.4	3.8	4.2	4.0	1.32	1.56	1.6	1.72	—
Length	137	418	119	155	78	102	115	80	53	72	120	330	—
Ratio	83.5	261.2	38.6	47.2	22.9	26.8	27.3	20.0	40.1	46.1	75.0	191.8	—

(A) — Bartonbury.

(B) — Trent Lodge.

The fertile tillers of the very early growth are sterile tillers of the previous season. Under exceptionally favourable winter conditions, dead, or partially dead leaves may retain their structure sufficiently well to permit measurements, and then the previous autumn's long narrow leaves contrast markedly with the shorter leaves developed by the new fertile tiller (Table 6).

Duval-Jouve (1875) and Arber (1934) have indicated that asymmetry about the mid-rib is found in *P. pratensis*, and this has also been recorded in *P. angustifolia*, and measurements for the fertile and vegetative tillers are given in Table 7. The close examination of leaf-blades also reveals a feature that is frequently found in other Gramineae, namely a slight kinking of the blade near the apex that probably results from being temporarily compressed in the top of the leaf sheath below.

TABLE 7.

Asymmetry in leaf blades of P. angustifolia. Measured in mm. on either side of mid-rib.

Origin	Fertile Tiller					Sterile Tiller		
	1	2	3	4	5	1	2	3
Waterlane	1.8	2.2	2.52	2.52	—	1.04	0.88	0.88
	1.6	2.12	2.00	2.00	—	1.00	0.80	0.80
Kemble	—	—	1.64	1.92	2.32	0.88	0.76	—
	—	—	1.56	1.84	2.24	0.76	0.64	—
Kemble	—	—	1.56	1.60	1.28	0.64	0.68	—
	—	—	1.44	1.52	1.20	0.60	0.64	—

The leaf-ratio values have been intensively determined for sterile tillers in some populations. The sampling of tillers during the autumn has been found to be most suitable owing to the death of the shorter younger leaves by that time, for this means that the lowest green leaf on the tiller is very long and gives high values which contrast with the lower values given by the *P. pratensis* form if recorded in the same way. Values for clones and populations of *P. angustifolia* and *P. pratensis* are illustrated in fig 1. It will be seen that there is considerable variation between and within clones as well as within the populations, and it is intended to study this feature more fully in sympatric populations of the two taxa.

The number of leaves actually formed on tillers varies; on marked tillers that survive the winter and eventually flower the maximum recorded number is 11, and the minimum is 8. An intensive study of leaf-production has not been made, but the rate of leaf-production in the field is not high, and vegetative tillers with only 4 visible leaves between May and October have been recorded.

Several details of leaf-characters are of further interest. The width of leaf-blades of material classified as *P. angustifolia* has always been less than 2 mm. for sterile tillers, though this is exceeded in fertile tillers and sometimes in transplants. The winter burn of leaf by frost is severe and can be so complete as to make the location of plants virtually impossible.

Evans (1949) has given the average number of living leaves on tillers of *P. pratensis* as 3.4, and indicates that there is little variation from this mean. In the present work it has been found that the number of leaves on the tiller varies little at a given time but does

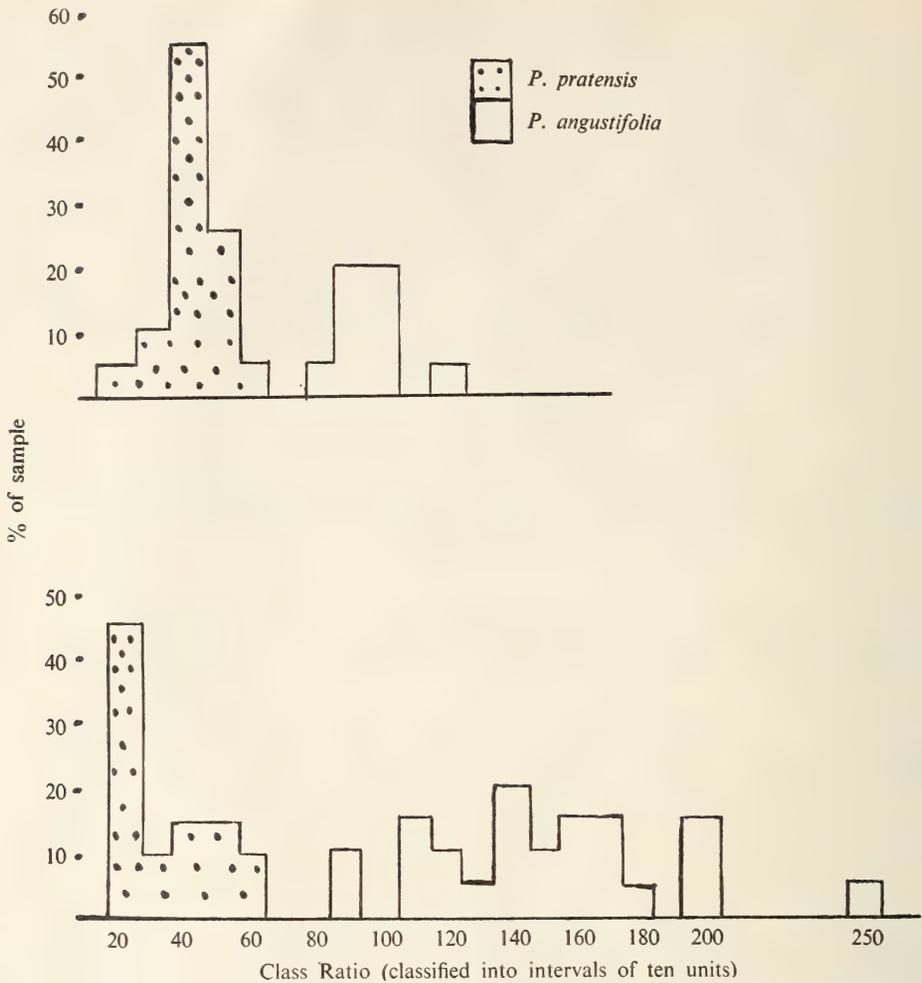


Fig. 1. Leaf Blade width : length ratios in clones and populations of *P. pratensis* and *P. angustifolia*.

so over the season as a whole (Table 8). Counts of leaves on the transplants showed a higher mean, and it is probable that lower competition and rate of leaf-death are responsible for this.

As the season advances, the sterile tillers of *P. angustifolia* produce new leaves at a slow rate and it is seldom that they become fertile during their year of origin. It is therefore,

TABLE 8.
No. of living leaves per tiller.

Centre	Date	No. of living leaves per tiller
Steadings Farm	18.6.56	1.88 ± 0.098
Three Mile Bottom	18.6.56	1.90 ± 0.078
Duddington	10.6.56	1.91 ± 0.076
Deer Park	18.6.56	1.82 ± 0.068
Deer Park	6.12.55	0.0*
Deer Park Transplants	18.6.56	2.82 ± 0.064

* All expanded leaves with burned portions.

very difficult to obtain measurements of the actual stem at the base of the tiller, and in order to obtain some quantitative data on tiller size it was decided to measure the length of tillers from the base to the tip of the sheath of the uppermost expanded leaf. In Table 9, some populations and seasonal variations are given which show the rapid increase in length obtained in the early part of the season.

TABLE 9. Sterile tiller length at various centres.

Centre	Date	Mean length of tillers in mm.
Shooter's Hill	26.5.56	52.3 ± 4.27
Royal Agricultural College	26.5.56	67.3 ± 1.67
Duddington	10.6.56	46.25 ± 2.70
Deer Park 1.	26.4.56	47.9 ± 1.47
2.	26.5.56	59.5 ± 1.78
3.	30.6.56	60.67 ± 1.77
4.	26.7.56	61.28 ± 1.39
5.	24.8.56	66.08 ± 3.45
6.	15.10.56	62.05 ± 5.01

Under greenhouse conditions the transplants may produce leaves well into November, whilst those outdoors have completed all visible growth, and these greenhouse leaves show a distinct shortening that is probably a result of decreasing day-length. Some measurements are recorded below.

Leaf-blade measurements of a greenhouse transplant ex Deer Park. D.P.1.

Month	Blade Length mm.	Blade Width mm.
September	211	2.04
	301	2.32
	250	2.48
October	176	2.32
	168	2.20
	150	2.20

The Culm and Inflorescence

The lengthening of the fertile tiller is due to internode-elongation. Measurements taken at different dates showed that elongation occurs in succession from the tiller-base, with each internode completing its elongation before there is any appreciable elongation of that above. Data, presented in Table 10, are similar to those recorded for various other Gramineae (Evans, 1927 ; Evans and Ely, 1941 ; Cooper, 1956), with internode-length increasing up the culm.

TABLE 10.
Elongation of fertile tillers at Deer Park. Internode length in mm.

Date	1.	2.	3.	4.	5.
26.4.56	0.9	1.0	45.1	8.1	—
5.5.56	1.4	46.0	87.0	9.0	2.0
14.5.56	169.0	130.0	90.1	10.1	2.1
20.5.56	280.0	146.0	90.5	10.0	2.0
14.6.56	212.2	149.3	91.5	10.2	2.1

The early elongation of the fertile tillers of *P. angustifolia* results in the maximum culm-height being reached by the end of May or early June. Samples for further culm-measurements were then collected when the panicle-branches had opened (Table 11.), and culm-diameter was measured just below the panicle and just below the second node down from the inflorescence.

TABLE 11.
Culm internodes at various centres,

Centre	Internode length in mm. Nodes in descending order.						Diameter mm.	
	1	2	3	4	5	6	1	2
Trent Lodge	260.9	163.0	69.0	11.0	1.0	—	0.676	1.352
Steadings Farm	266.7	161.9	58.7	6.9	2.7	2.0	0.776	1.520
Deer Park	212.2	149.3	91.5	10.2	2.1	—	0.692	1.180
Shooter's Hill	227.9	141.0	77.2	9.2	1.7	—	0.648	1.356
Duddington	253.0	124.7	45.1	8.0	1.4	—	0.760	1.440

The inflorescence data recorded for various populations (Table 3) clearly show variability in length of panicle and number of branches at the lowest node. At Deer Park some additional observations showed the mean number of spikelets per panicle to be 115.20 ± 7.30 and the mean number of florets per spikelet as 4.03 ± 0.09 during the 1954 season.

The inflorescence of *P. angustifolia* is much branched, and in addition to recording the number of branches at the lowest node for various populations (Table 3), the number of branches at each node were counted in some cases (Table 12). The number of branches was higher at the first few nodes and decreased to one at the last few nodes ; the length of internodes decreased up the panicle and the number of nodes varied within and between plants.

TABLE 12.
Branches per node of the panicle at Deer Park.

Plants	Branches per node and node number.														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Wild average	4.4	4.2	3.7	3.4	2.6	2.2	1.9	1.7	1.1	1.0	1.0	0.9	0.7	0.3	—
Transplant average	4.7	5.0	5.0	4.9	4.3	3.9	3.5	2.8	2.1	1.7	1.3	1.1	1.0	0.8	0.3
Variation in 3 panicles of transplant 1.	4	4	5	4	4	3	2	2	2	1	1	1	1	1	—
	5	5	5	5	4	4	3	3	2	1	1	1	1	1	—
	5	5	5	5	4	4	3	3	2	1	1	1	1	—	—

In the present work it was found that the truly narrow-leaved individuals had three nerves on the upper glume and one nerve on the lower glume, though slight differences were sometimes found within panicles.

FLORAL BIOLOGY

Anthesis in *P. angustifolia* has been studied under greenhouse and field conditions, and commences about two thirds of the way up the inflorescence, at the fifth to sixth node from the top. Further spikelets come into anthesis above this point and then downwards from this point occurring at the lowest node last of all. The occurrence along the branches is variable, usually the lowest spikelets opening first.

Basal florets of a spikelet open first, eventually followed by the others in ascending order, though the topmost floret may not open at all. The actual opening of the florets is variable: in some cases, stigmas spread first, and, in others in the same panicle, anthers may appear before the spread of the stigmas. The anthers are suspended clear of the pales on white, fine filaments, and eventually split along their length. The anthers are often tinged with purple and one may lag behind the others in elongation. In general, however, anthers and stigmas appear roughly together. Anthesis was first recorded in one plant at 10 a.m., in others as early as 6.30 a.m., B.S.T. Anthesis proceeded throughout the morning. One floret first opened at 10.0 a.m., stigmas were extended at 11.0 a.m., two anthers fully emerged at 12.30 a.m., and all three stamens fully elongated by 2.0 p.m. Observations at night showed florets open.

Pollen-fertility was determined for transplants and field material by making aceto-carminic squashes of anthers when adjudged fully ripe. Size of pollen grain was measured at the greatest diameter on shed pollen as the pollen grains were not all perfectly round. Fertility was always high and diameter variable (Table 13.).

In several plants pollination was studied in open and enclosed panicles. Whole ovaries were removed and stained in aceto-carminic and mounted in 45% acetic acid for observation. Permanent preparations were made in some cases by dehydration and mounting in Euparal. Pollen grains with smooth walls were readily seen and pollen-tubes could easily be seen where germination had taken place. Tube-cytoplasm was weakly stained but staining with either Iodine or Cotton Blue gave no better results, usually, in fact, less satisfactory ones. Pollen-tubes were never actually seen to penetrate the body of the ovary.

Pollen was readily shed by movement of the panicle and the general behaviour was typical of that of cross-pollinating grasses.

TABLE 13.

Pollen diameter and fertility in Deer Park wild plants and transplants.

<i>Plants</i>	<i>Pollen Diameter *</i> μ	<i>Range</i> μ	<i>% unstained **</i> <i>pollen</i>
Deer Park	31.51	22.8 — 42.4	4.10
6 Transplants	28.46	24.0 — 33.6	8.60
	27.93	21.6 — 31.2	2.45
	28.05	19.2 — 31.2	6.70
	27.26	19.2 — 33.6	4.00
	29.90	19.2 — 45.6	8.80
Deer Park	27.21	19.2 — 30.0	5.00
4 Wild Plants	26.93	22.8 — 33.6	6.80
	27.05	19.2 — 33.6	9.50
	23.40	21.6 — 32.0	8.60
Duddington Wild Plant	26.83	24.0 — 31.2	9.26

* 50 grains per plant

** minimum 300 grains per plant.

TABLE 14
Seeds/Panicle of selfed and open pollinated plants.

Plants	Open Pollinated	Self Pollinated
Deer Park 1.	322	314
transplants 8.	302	221
5.	320	239
3.	448	45
Trent Lodge	440	56
	386	330
Waterlane	421	382

Once the body of the ovary commenced to enlarge the pales closed. Removal of the ovary made little difference except that large numbers of ungerminated pollen grains might be found.

On ripening, seed was harvested from individual panicles, and open and self fertility data were estimated for transplants and field material. Open fertility was high, and self-fertility variable, being very high in some plants (Table 14).

Normal seed production in the field was determined from Deer Park in 1953 as 412.10 ± 29.30 per panicle. Seed-weight was also determined at Deer Park as 0.00025 grms.

CYTOLOGY

Apomictic and sexual reproduction has already been demonstrated in *P. angustifolia* by Åkerberg (1941), who also provides chromosome numbers of an aneuploid range of $2n = 50 - 65$. The chromosome studies in this work have all been on established material of wild origin. Root-tips have been stained in Feulgen and give small metaphase plates with high chromosome numbers. Owing to the density and the smallness of the chromosomes, accurate counting was not possible. The following numbers were calculated :—

Source	Number
Deer Park	c. 52
Deer Park	c. 60
Deer Park	c. 58
Bagedon	c. 61

Meiosis has only been studied in pollen mother cells. Feulgen staining gave variable results but some of the clearest views of metaphase and anaphase of the first division. Aceto-carmine squashes were useful but cytoplasmic staining was troublesome whilst aceto-orcein gave good results. However, pairing was regular and the number of univalents observed was small, being 3.9 ± 0.37 . This is in general agreement with the figures given by Nygren (1951) for the other *Poae*. The high pollen-fertility also indicates that this univalent formation is insufficient to disturb the efficiency of pollen formation. The univalents lag during anaphase, usually lying on the metaphase plate and dividing late. Cross-wall formation is often found, with these univalents or their products isolated from the haploid nuclei, and lagging is again found at the second division with univalents excluded at tetrad formation.

TRANSPLANTS

In a critical group such as *P. angustifolia*, it is essential to use transplants to study variation, and material has been collected from Deer Park, Kemble, Waterlane and Duddington, but only in the first has an extensive range been studied. Some data have already been discussed and the quantitative increases of characters noted (Table 4.).

Habit. Two main forms were found : first a tufted dense habit with erect tillers and slight rhizome development; and second, a looser, more open habit with suberect tillers and a greater rhizome production. The former was considered typical of *P. angustifolia* and the latter extreme.

Leaf Blade. On the sterile tillers these are narrow and long, though both short narrow-leaved and long wider leaved forms were found. The leaf-length varied up to 42 cm, and the width from 1.2 — 2.5 mm. under these transplant conditions.

Tillers. Tiller-width varied according to the width of the sterile leaves and rhizome length was also variable within and between plants.

Inflorescences. These varied in length within and between plants, similar variations being found in the number of nodes and the number of branches per node. The number of nerves of the upper glume was three, on the lower, one, though some variation was found within the panicles.

Phenology. The greatest variation was found in the time of panicle emergence and time of rhizome formation, there being :-(a) Variation in the emergence of the first panicles of the order of four weeks, resulting in the overlapping with forms of *P. pratensis* though these were always later on all stages of emergence and elongation of the culm. (b) Rhizomes were formed after panicle emergence and late appearance of the panicle was associated with later rhizome production. (c) Anthesis was variable but there was less difference between plants than found in the other stages; although forms of *P. pratensis* may produce panicles later there is much overlap of anthesis with *P. angustifolia*.

General Considerations. The transplant studies showed that there was considerable genetic variation within populations on a morphological and phenological basis, and in no certain way offered any means of avoiding subjective methods of classification. This variation could be arbitrarily classified into two groups as follows :—

(a) The tufted, early-flowering plants with very narrow leaf blades on the sterile tillers. These vegetative features were considered as the focal point of the *P. angustifolia* type and such plants were easily separated under field conditions, even where other forms of *P. pratensis* were present. Inflorescences had one-nerved lower and 3-nerved upper glumes.

(b) The more open, slightly creeping plants with a variable flowering time that had somewhat broader leaves under transplant and field conditions and formed a very small percentage of most populations. Blade-width was approximately 2.0 — 2.3 mm. under cultivation and about 2 mm. in the field. This group approached the *P. pratensis* group in its appearance and was considered to be an extreme form of *P. angustifolia*.

Whilst it must be emphasised that subjective techniques of classification are necessary in the group and therefore that the precise taxonomic limits are matters of opinion, the importance of the phenological data must also be stressed, for it has clearly shown that the very narrow-leaved forms are characteristically early spring forms and thus that *P. angustifolia* is a definite physiological form. This is all the more evident when comparisons are made with the *P. pratensis* group.

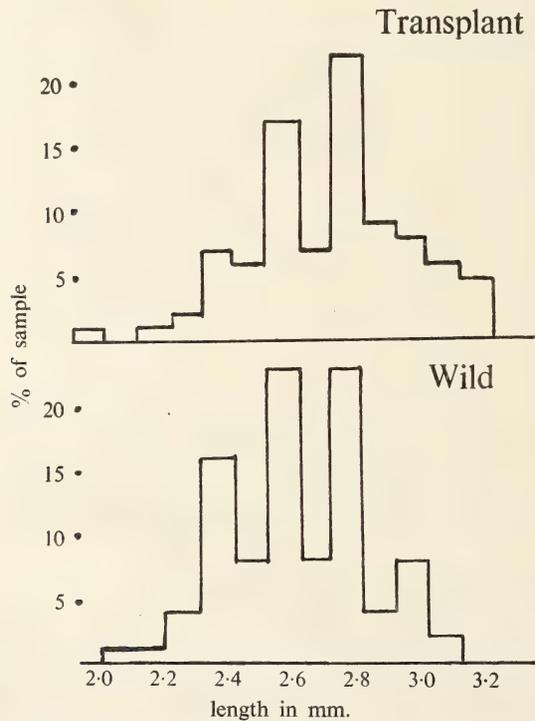
TABLE 15.

Germination and polyembryony in P. angustifolia.

Centre—or plant	Germination %	Seedlings/caryopsis				Polyembryony %
		1.	2.	3.	4.	
Deer Park	87.5	313	60	4	—	8.0
1955 Hailey Farm	88.0	144	8	1	—	4.5
General Sample	67.2	309	24	2	1	5.4
Deer Park general	83.0	76	5	2	—	7.0
Deer Park selfed 5	80.0	34	6	—	—	12.0
8	86.0	41	2	—	—	4.0
1956 1	60.0	27	3	—	—	6.0
Deer Park open 5	83.0	80	3	—	—	3.0
8	86.0	82	4	—	—	4.0
1	84.0	82	4	—	—	4.0

GERMINATION AND POLYEMBRYONY

Seed samples were collected from several centres during 1955 and a general bulk sample was also harvested from a wide area of the Cotswolds. All samples gave a high germination and in all cases there was a percentage of multiple seedlings (Table 15). Further data were collected for the 1956 season as well as for individual transplants. The polyembryony, that is evident for the various samples, is of well known occurrence in

Fig. 2. Seed length in wild and transplant *P. angustifolia* ex Deer Park.

P. pratensis, and, in the present work, the effect of competition on seedling size and development within multiple groups was obvious. The highest multiple association recorded was four, with twin seedlings the most common. Seed-length was measured in wild and transplant populations (Fig. 2).

SEEDLING MORPHOLOGY AND ESTABLISHMENT

Preliminary studies of morphology have been made on the following characters under greenhouse conditions; rate of germination, rate of leaf emergence, rate of tillering, leaf-blade width and length on the main tiller, tillering of secondary tillers and the appearance of rhizomes. Seed was collected from heads of *P. angustifolia* and sown in seed boxes and 3-inch whale-hide pots. In the boxes, seed was sown thickly in rows as well as spaced individual seed. Multiple seedlings were discarded.

The rate of germination was fairly even and sowing on 13.4.56 resulted in the emergence of the coleoptiles within ten days, the first leaf emerging 2 or 3 days later, the first tillers being recorded 30 days after sowing. No tillers were visible on the seedlings until at least 3 expanded leaves were developed, and two secondary tillers were obtained in the fourth leaf stage, whilst the third tiller was found in the fifth leaf stage. A small number of tillers developed from the axils of the coleoptiles, but, on the majority of plants in this series, the first tiller appeared in the axil of the second leaf often followed by the second tiller in the axil of the first leaf. The third tillers all arose in the axil of the third leaf.

Seedling competition in the present series was studied on thickly sown plants, and, 47 days after sowing, there were three more tillers on the pot-sown plants (Table 16).

There was a progressive increase in the length and width of successive leaves. Tillers arose from the secondary tillers when they had three leaves and were found in the axil of various leaves.

During these observations it was found that all the seedlings were not of the same habit type, that nearly all were hairy-leaved, and that a few plants were very broad-leaved. (3rd. leaf 3 mm.) and resembled seedlings of the *P. pratensis* complex.

DISCUSSION

The taxonomic complexity of *P. pratensis* (Gustafsson, 1947; Stebbins, 1950; and Melders, 1955) suggests that the *P. angustifolia* complex can be regarded as one of at least four types that are linked by intermediate forms. This suggests two main problems, first, the field characteristics and general taxonomic limits of the group, and secondly, the means whereby these limits are maintained. As phenotypic variation within the populations is considerable, the use of transplants is a necessary part of these studies, and the wide range of sward types, in which the complex is found, necessitates sampling in as wide a range of areas as possible.

P. angustifolia is a colonist of poor grasslands, the rough swards of agricultural land, and road verges. However, the complexity of agricultural practices is such that all intensities of biotic pressure are to be found within limited areas, so that it is common to find the *P. pratensis* complex in the same or adjacent swards, and so within cross-pollination range. This introduces problems of taxonomic status in such populations, and makes it a necessary associated study of the *P. angustifolia* complex. The precise morphological limits of *P. angustifolia* in these, and all areas, are of immediate concern, and are made difficult by the fact that some populations, although containing a high percentage of typical narrow-leaved *P. angustifolia*, contain a very small number of types not satisfactorily included in that group. They exhibit various morphological and physiological differences which may indicate hybridisation with other sympatric complexes, and, owing to the

results of phenological studies of transplants, it was decided to collect only plants with narrow leaf-blades and well defined tufted growth as typical of *P. angustifolia*. It is therefore obvious that subjective techniques immediately enter the work, and, although these are often present in taxonomic work, they are somewhat sharpened in this case by the taxonomic difficulties of *P. pratensis* already fully discussed by Åkerberg (1942) and Nygren (1954), and made prominent by the work at the Carnegie Institution. It is not intended to reconsider these points here, but merely to indicate that, in this study, they are problems confined to single populations. Indeed the exploitation of the same habitat by what are regarded by some workers as subspecies of a polymorphic species, is one of the interesting features found in the Cotswold grasslands.

The opinion built up is that *P. angustifolia* is physiologically adapted not only to drier soils (Åkerberg, 1941; Hultén, 1950) but also to areas of low biotic pressure, the rough grasslands of agricultural areas. There is a marked absence in intensively managed areas where certain *P. pratensis* forms become prevalent and persistent. The phenology of the type, with its early and short period of vegetative growth followed by little growth in late summer and autumn, is well adapted to poorly managed areas. Detailed phenological studies show interesting features as follows:—(1) An early production of fertile tillers with broad leaves. (2) Elongation of fertile tillers accompanied by tillering of vegetative shoots with narrow leaf-blades from the base. (3) Early panicle emergence. (4) Rhizomes produced after panicle emergence, so that, in the early season an essentially tufted appearance is obtained above ground. (5) A poor period of vegetative growth in summer and autumn. The plants are early short season types, with almost complete die back in severe winter weather. Thus, whilst the group is taxonomically different in many ways from the *P. pratensis* complex, it can also be regarded as physiologically different in that it has earlier panicle emergence, poor post-emergence tillering, and negligible summer and autumn growth. In addition there is much genetic variation, as transplant studies have shown.

The chromosome numbers are difficult to count accurately (Åkerberg, 1942) and in the present work the following range has been recorded, $2n = c. 52 - c. 61$ and shows variation within populations. Meiosis in pollen mother cells has been studied and the presence of small numbers of univalents indicates aneuploidy, but it is insufficient to affect pollen-fertility as this is high. Floral biology suggests that cross-pollination is normal, but there is much evidence for apomixis as selfing gives high seed-yields in some individuals. Pollen is easily found on stigmas of self- and open-pollinated plants with the pollen tubes well developed, and aceto-carminic squashes of enlarging ovaries have been found in which there is no visible trace of pollen-tube penetration of the ovary body. This, however, does not preclude the presence of sexual reproduction, and both forms are reported on Swedish material by Åkerberg (1941). It is possible that apomixis is common as high self-fertility has been obtained, whilst the occurrence of polyembryony and aneuploidy support this view. In addition, progeny raised from randomly selected selfed seed of No. 1 Deer Park transplant, are, to the eye, identical in appearance, and are presumably the result of apomixis. Also, there is a considerable amount of rhizome production that would multiply the biotypes that establish in any sward, and do a great deal towards balancing any low establishment from seed.

At this stage it is worth considering the breeding mechanism of the complex at the population level, for it will considerably influence the genetics and taxonomy of the group. It has been recorded that seed-production per panicle is high both in the field and in transplants. However, when panicles are enclosed self-fertility is seen to vary considerably. It appears that in the majority of plants self-fertility is high but in a small proportion it is poor but does give a small yield, which may indicate the presence of a normal sexual reproduction. One of the obvious effects of this apomixis is an assured seed production,

which is accompanied by a reduced gene-exchange and reduced segregation of new genotypes. However, the presence of sexual reproduction in some plants would give an opportunity for the appearance of new gene-combinations that could be subject to ecological selection, and so endow the population with a versatility of breeding mechanism. Thus apomixis could rapidly multiply well-adapted forms, and the sexual process produce forms that might well be of value under different ecological conditions. In addition, the production of rhizomes would permit the easier spread of suitable biotypes in these dense and competitive grassland conditions than would be possible by seed.

The net effect would be to limit gene-exchange even within the relatively narrow limits of the population, and to limit also hybridisation with other ecological forms or subspecies of *P. pratensis* that, owing to the nature of agricultural activities, would be almost certain to be sympatric.

Thus apomixis coupled with the ecological specialisation of the complex would account for much of the taxonomic differentiation, whilst the possibility of sexual reproduction would permit the maintenance of variability by segregation following either hybridisation within the complex or with related and sympatric complexes. Clausen (1952) has reported that there is much variation between the survival rates of apomictic and sexual progeny in *P. pratensis*, and this might be very effective at the inter-complex level, and so reinforce the ecological specialisation. But this theoretical discussion can be only resolved by the detection of inter-complex hybrids by subjective field taxonomy or by their artificial production. There are seedling differences between the *P. angustifolia* and *P. pratensis* groups, and it may be possible to express these quantitatively, as Saeed (1956) has done in the agricultural strains of *Lolium perenne* at the seedling stage. Quantitative studies of the leaf-blade width : length ratios and other taxonomic details might supplement subjective taxonomic methods in sympatric populations, where the detailed and very wide hybridisations within the *Poa*e reported by Clausen *et al.* (1947 - 1953), would lead to an expectation of inter-crossing.

Thus the extremely widespread distribution of *P. angustifolia*, and the presence of forms approaching the *P. pratensis* complex have shown characteristics that are well appreciated for other sections of the species (Åkerberg, 1941 ; Nygren, 1954), and at the same time introduced several eco-taxonomic problems of essentially local interest. Thus at the population level it has been obvious that there is considerable morphological and physiological variation within the taxon, and it has been necessary to resort to detailed transplant studies to obtain satisfactory analysis of the population variation where *P. pratensis* forms are present and intermediate types are suspected, and it is intended to give a further account of work on these sympatric populations. However the tufted nature of the centre parts of the plants and the narrow leaf-blades of the sterile tillers are, together with the early panicle emergence, the main characteristics of the complex. There is much therefore to confirm the view that *P. pratensis* is a polymorphic species consisting of several focal types or ecological population-complexes which may hybridise to give intermediate forms, but more detailed work is needed on the other Cotswold forms of the *P. pratensis* complex before a more reasonable assessment can be made. Thus a study of the other British subspecies of *P. pratensis sensu lato* and also the location and study of communities where they are sympatric may give a clearer picture of the eco-taxonomy of the complexes.

SUMMARY

Populations of *P. angustifolia* are of widespread occurrence in rough Cotswold pastures and on road-verges, being associated with such species as *Bromus erectus*. It is absent from hard grazed areas where *Lolium perenne* is abundant. The distribution mosaic of agricultural management results in considerable overlap with various forms (subspecies) of *P. pratensis* even within the same field.

P. angustifolia populations in rough swards show considerable variation and a small proportion of related forms are not satisfactorily included in the *P. angustifolia* complex. Transplant studies are being conducted on these variants which are very similar to *P. subcaerulea*. Variation in tillering, leaf-blade size and width, inflorescence and reproductive characters is found in *P. angustifolia*. Seed production is high but rhizome production is not great under field conditions.

Phenological studies show severe winter die-back and early spring development of fertile tillers with broad leaf blades in which panicle primordia are found in late February and early March. Elongation of the fertile tillers is accompanied by production of vegetative tillers with very narrow leaf blades. Panicle emergence occurs in April and early May, and culm elongation is the result of successive internode elongation with the topmost internode the longest. Rhizomes are produced after panicle emergence.

The sterile tillers increase in length in early spring and reach their maximum by mid-summer. The number of living leaves per sterile tiller is small, ranging from 1 to 3. The life of sterile tillers varies, sometimes being short, 2 or 3 months, but usually extends into the following season when fertile tillers develop from some of them. In these fertile tillers leaf-blade characteristics alter conspicuously as the leaf-blades are much broader on the culm. All leaf blades show asymmetry about the midrib. The plants or tufts are thus in a constant state of change from season to season having few truly perennial or completely persistent shoots.

Pollen-fertility is high and anthesis is typical of cross-fertilising species. Self-fertility is variable but usually very high. High chromosome numbers are found and P.M.C. meiosis shows occurrence of univalents. Polyembryony is common. There is evidence consistent with apomixis in some plants.

An account of seedling morphology is given and it is possible that there may be real quantitative differences between *P. angustifolia* and other forms of *P. pratensis* at this stage.

Transplant and field studies have emphasised the need for careful analysis of *P. angustifolia* where it is associated with other forms of *P. pratensis*.

P. angustifolia is essentially a colonist of well-drained soils subjected to low intensity of agricultural management, and its early but short season of active growth is well suited to such areas. It is therefore a distinct physiological type or ecological complex, within which a versatile breeding mechanism allows apomixis rapidly to multiply well-adapted biotypes whilst the sexual reproduction of other forms permits hybridisation and the segregation of new genotypes. Apomixis is probably the means whereby it maintains taxonomic distinctness in habitats in which other forms of *P. pratensis* may be in physical contact with it.

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GENTIANELLA IN BRITAIN

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I. *G. AMARELLA*, *G. ANGLICA* and *G. ULIGINOSA*

INTRODUCTION

The genus *Gentianella* Moench is widely spread throughout Western and Central Europe and America. In all parts of its range it poses taxonomic problems. The reasons for this are at least four in number. First, between some of the species extensive hybridisation occurs, which may result in more or less complete introgression. Secondly, any single population of some species may contain both annuals and biennials, which are frequently different in such characters as habit and leaf-shape. Thirdly, local populations show great variability in morphology, which can partly but not entirely be related to the first and second reasons. Fourthly, there is considerable variation between separate populations in small geographical areas.

These points are all shown by the British representatives of the genus, which have for some time been regarded as taxonomically difficult species. Species such as *G. anglica* (Pugs.) E. F. Warb. and *G. uliginosa* (Willd.) Börner are relatively distinct, but there is much confusion within the aggregates *G. campestris* (L.) Börner and *G. amarella* (L.) Börner.

The situation outlined above suggests an experimental approach to the problems, but the extreme difficulty of germinating the seeds has rendered such an approach impossible. Other workers, notably Favarger (1953), have experienced similar difficulties. Because of this, it has been necessary to employ certain statistical methods for the morphological analysis of both single populations and existing herbarium specimens.

Four main problems have been considered. These are :

- I. The variation in *G. amarella* and the relationship between that species and *G. anglica* and *G. uliginosa*.
- II. The variation within *G. septentrionalis* (Druce) E. F. Warb., and the relationship of that plant to *G. amarella*.
- III. *G. germanica* (Willd.) Börner and the hybrid populations of that species and *G. amarella*.
- IV. The identity and relationship of *G. campestris* (L.) Börner and *G. baltica* (Murb.) Börner.

I. SUMMARY

An investigation of random samples and existing herbarium material of *G. amarella* by simple statistical methods has revealed that the British species agrees with Linnaeus' type specimen in the Linnaean Herbarium; these are therefore, *G. amarella* subsp. *amarella*. They can be divided into four or perhaps five regional "races", defined on comparatively small morphological differences and differences in geographical distribution.

The Irish plants of *G. amarella* are described as a new subspecies, *G. amarella* subsp. *hibernica*.

The variation within *G. anglica* is examined and those plants found on the N.W. coast of Cornwall are found to be distinct from the main body of the species, including Townsend's type from the Isle of Wight (Townsend, 1883). They are described as a new subspecies, *G. anglica* subsp. *cornubiensis*.

The South Welsh populations of *G. uliginosa* are considered in relation to the European forms described by Willdenow (1797). Lack of sufficient material has prevented a very full comparison. A new hybrid, *G. amarella* × *uliginosa* is described.

2. EXPERIMENTAL WORK

A number of attempts has been made to cultivate species of *Gentianella*. No results were obtained with *G. septentrionalis*, *G. uliginosa*, *G. germanica* or *G. campestris*, either in the field or in pot experiments. The results of pot experiments with *G. amarella* and *G. anglica*, though scanty, are of some interest, especially when combined with the results of extensive field observations.

Seeds of *G. amarella* gathered from localities in N.E. Yorkshire and in Berkshire were sown in pans containing either natural chalk soil from the Chilterns (Ivinghoe Beacon) or John Innes Seed Compost. In the Ivinghoe Chalk soil germination was moderate (about 15%). In all cases the plants became chlorotic and died before passing beyond the cotyledons plus four leaves stage. In J. I. compost germination was much poorer, but the seedlings produced proceeded to the flowering stage, producing healthy plants. Attempts to transplant the Ivinghoe seedlings to John Innes Compost were unsuccessful. In open ground plots in a variety of habitats, no germination occurred, even though in one habitat seedlings of *G. amarella* growing locally appeared.

The seed was sown on 17 December 1954, and the pots placed in a cold frame left open to the frost and snow, but not to heavy rain. By 18 April 1955 crops of seedlings had appeared in the Ivinghoe soil, and consisted of the two cotyledons. By 20 June 1955, many of these had vanished, and those that remained were in an unhealthy condition. By the latter date 5 seedlings had appeared on the J. I. compost, and consisted of the cotyledons and two pairs of leaves, forming rosettes about $\frac{1}{4}$ " across. By 10 December 1955 these seedlings had reached a size of $\frac{1}{2}$ - $\frac{3}{4}$ " and the leaves were dying off. By 26 June 1956 all 5 plants had formed new rosettes, and were raising flowering spikes. All produced seed.

Over the same period, a close watch was kept over a number of natural populations in Oxfordshire, Berkshire and Yorkshire, while less complete data were gathered from other localities. From these observations it is clear that *G. amarella* seldom, if ever, occurs in exactly the same spot for two years running, although it may occur only a few yards away. Thus, at Beacon Hill, Oxon., an area of about 1 acre was thickly covered with plants in full bloom in September 1955. In the same area in September 1956 only about 100 plants were flowering and there were no seedlings visible. The "peak" years for different populations are not the same, since at Letcombe Bassett, Berks., about 25 miles from Beacon Hill, there were far more plants in 1956 than in 1955. It appears that there is a long period of dormancy in the seeds, which accounts both for the failure of the culture experiments (at least in part) and for this sporadic occurrence.

In some instances rosettes have been seen in late summer and autumn, clearly belonging to first-year plants. Coupled with the results of the culture experiments, this indicates that the plants are true biennials (as is normally accepted) germinating in the spring, dying away to a small underground bud in early winter, and renewing growth in the spring. Soon after flowering the plants die. In no herbarium specimens of pure *G. amarella* has

any indication of other than biennial habit been seen. The indications of biennial habit are the absence of cotyledons and the different forms of the rosette leaves of the first and second years. In the first year these are normally lanceolate or ovate-lanceolate, while in the second year they have the more characteristic shape of spatulate, obovate or oblanceolate, seen in herbarium specimens.

Seeds of *G. anglica* from populations in Dorset and Lincolnshire were sown on the soils already described under *G. amarella*. The behaviour of the seeds was almost exactly parallel in the two cases. All the seedlings in Ivinghoe soil died, while by 20 June 1955 two healthy seedlings had appeared in the J. I. Compost. These two plants, by then about 1½" diameter, died down in December, and started growth at the end of January, eventually flowering about the beginning of June. Both produced seed. Field observations in Surrey and Berkshire suggest that fluctuations occur in populations of *G. anglica* in a very similar way to those in *G. amarella*.

The phenology of *G. anglica* has been much disputed. Townsend (1883) in the original description considered that grazing prevented the plants from flowering in the late summer, like *G. amarella*, but enabled them to flower early the following year. Marshall (1892), on the other hand, saw the plants "springing up in seedling form" at Durlston Head, Dorset, in the spring. (I have observed 2nd year rosettes in February, in Surrey; it seems clear that Marshall mistook these for young seedlings.) Bennett (1892) observed germination near Croydon in autumn, and he watched the plants through the winter up to the flowering stage in May or June. This agrees with the experimental results already outlined, except that germination occurred in spring or early summer in the plants grown in pans. (In some of the pans a few seedlings appeared in the autumn, though these died during the winter, and it is possible that time of germination may vary.) In general, *G. anglica* behaves in a similar way to *G. amarella* (i.e. as a biennial), except for its earlier flowering and a possibly earlier start into growth in spring.

In the germination experiments with *G. uliginosa* no seedlings were obtained. One natural population at Oxwich, Glamorgan, covering a small slack of about 150 sq. yds. area, has been observed in some detail. In August 1955 there were about 100 plants in full flower, clearly biennials in their second year. No signs of first year plants were seen. In the following November these plants were dead, though they still contained seed in their capsules. In addition there was a fair sized crop of small annual plants, consisting of little more than a rosette of 4-8 leaves and one, or rarely two, flowers. In March 1956 there was no sign of either seedlings or first year rosettes. Seven months later, in October 1956, there were a number of dead plants (biennial) and again a very large crop of small annuals in full flower.

The behaviour of *G. uliginosa* appears to be egregious. There is a tendency to behave as *G. amarella* does, as a normal biennial. The observations of Lousley (1950) suggest that at least some of the large autumn-flowering plants are annuals, germinating in the spring of the year in which they flower. However, no seedlings were seen in March 1956. The small October-November flowering plants, belonging to the same population, appear to be annuals, and I consider that they may have grown from seeds sown by the August plants of the same year: i.e. their whole life-cycle occupied only 2-3 months. In the damp, sheltered and sunny conditions in which they are found this does not seem impossible, though it is perhaps more likely that the plants are produced from seeds which have lain dormant in the soil for some time. Further observation on this point is desirable, coupled if possible with cultural experiments. The occurrence of annual and biennial plants in the same population is paralleled by *G. campestris*. This hypothesis is difficult to reconcile with the negative results of the pot experiments, and until a method of germinating the seeds has been found it must remain very tentative.

3. ECOLOGY AND DISTRIBUTION

Gentianella amarella (L.) Börner.

G. amarella is restricted to two types of habitat. These are grassland on chalk, oolite, magnesian limestone and carboniferous limestone, and mature slacks in grey dunes in N. Devon, Wales, Lancashire, Scotland and possibly N. Norfolk and Lincolnshire. These habitats are characterised by a markedly calcicolous flora.

G. amarella is almost invariably found in short turf in open habitats, away from shrubs and scrub. Where, since the onset of myxomatosis, the vegetation has grown longer, often with strong invasion by such grasses as *Brachypodium* sp., *G. amarella* disappears. This has been noted, for example, at Wytham (Berks.), Freshfield (W. Lancashire) and Wass Bank Top (N.E. Yorks.). Among the most frequent associates of *G. amarella* are: *Carex flacca*, *Euphrasia* spp., *Festuca* spp., *Hieracium pilosella*, *Linum catharticum*, *Lotus corniculatus*, *Plantago lanceolata* and *Thymus drucei*.

Gentianella anglica (Pugs.) E.F. Warb.

Except for the fact that it is almost completely restricted to the chalk, the general ecology of this species is very similar to that of *G. amarella*. It frequently occurs in even more exposed positions, where the depth of soil is only 1-2", often with considerable exposure of the bare chalk. *G. anglica* often occurs on steeply sloping ground rather than on the level, a difference most obvious when it and *G. amarella* grow together. Among the plants commonly associated with *G. anglica* are *Asperula cynanchica*, *Briza media*, *Festuca* spp., *Galium verum*, *Helictotrichon* spp., *Hieracium pilosella*, *Linum catharticum*, *Lotus corniculatus*, *Poterium sanguisorba* and *Thymus drucei*.

Gentianella uliginosa (Willd.) Börner.

G. uliginosa is geographically restricted to such an extent that any generalisations are of limited value. Willdenow (1797) gives its habitat as "in pascuis udis", and it seems that on the Continent it is found in inland marshes. In Britain it occurs only in dune slacks, which appear to vary considerably in the height of the water table. Its habitats are the same as those of *G. amarella* in South Wales, and are characterised particularly by *Carex flacca*, *Euphrasia* spp., *Festuca* spp., *Leontodon autumnalis*, *Lotus corniculatus*, *Ononis spinosa*, *Plantago maritima*, *Prunella vulgaris*, *Salix repens* and *Viola canina*.

4. BIOMETRIC WORK

Gentianella amarella

G. amarella has long been regarded in Europe and in Britain as a taxonomically difficult species. Murbeck (1892) and Wettstein (1896) both divided it into two subspecies (subsp. *axillaris* (Schmidt) Rchb. and subsp. *lingulata* (C.A. Agardh) Murb.) and stated only the former occurred in Britain. This appears to be true, but subsp. *lingulata* occurs as a distinguishable taxon on the Continent, and it is referred to later.

A preliminary survey of the whole *G. amarella* aggregate occurring in Britain (*G. amarella* s.s., *G. anglica*, *G. uliginosa* and *G. septentrionalis*) indicated a number of quantitative characters showing a considerable variation. On further investigation many of these were found to be of little value, and these are not described here. Those which were used in the biometric work are considered below; the data are for both random samples and herbarium specimens.

(1) Number of Internodes

The average number of internodes in the aggregate ranges from 0.3 in *G. uliginosa*, from 1.4 in *G. anglica*, from 2.7 in *G. septentrionalis* and from 4.11 in *G. amarella*. The character is of some use to distinguish species but it is also valuable at the infraspecific levels. It can be used as an absolute quantitative value, since it can be shown that it does not, within any taxon, depend on the size of the plants involved.

(2) Relation of terminal internode to the average length

The terminal internode varies considerably, being much reduced in some plants of *G. amarella* and *G. septentrionalis*, and elongated in *G. anglica* and *G. uliginosa*. Its actual size varies with the size of the plant, and it is best expressed as the ratio $\frac{\text{Average Internode length}}{\text{Terminal Internode length}}$.

For convenience in handling the logarithm of this value is used. Since the ratio is often less than unity (e.g. in *G. uliginosa* it is invariably so) the logarithm is increased by unity to give positive values in all cases. The expression used becomes :

$$\left(\text{Log } \frac{\text{Average Internode length}}{\text{Terminal Internode length}} \right) + 1.$$

(3) Leaf Shape

Two expressions of leaf shape were used. The simpler, length/greatest width (L/W), expresses the shape of the leaf in general terms, and is often sufficient used alone. In some cases, particularly in *G. septentrionalis* and *G. amarella* × *germanica* hybrids, it does not give sufficient expression of the leaf-taper, and after experiment the second expression was chosen. This is obtained by dividing the difference between the width $\frac{1}{4}$ of the distance from the insertion of the leaf (B) and that $\frac{1}{4}$ of the distance from the apex (A) by twice the length, the result being expressed as a percentage.

$$\text{i.e. Leaf index II} = \frac{B - A}{2L} \times 100.$$

Thus, in lanceolate or ovate leaves the expression is positive, in linear leaves zero and in obovate or spatulate leaves negative, while the magnitude of the expression indicates the degree of taper.

Since the number of internodes is variable, the choice of a representative leaf is more difficult. Normally, this has been a stem leaf two internodes below the lowest axillary flowers (not branches) but this occasionally has to be modified.

(4) Corolla length

Except in very reduced specimens the corolla length is independent of the size of the plant, and can be used as an absolute measurement. It is measured from the insertion of the corolla to the tips of the lobes, which are equal or subequal.

(5) Corolla/Calyx ratio

In *G. uliginosa* the calyx is often almost or quite as long as the corolla, in *G. amarella* it is usually between $\frac{1}{2}$ and $\frac{2}{3}$ of the length, and in *G. germanica* it is between $\frac{1}{3}$ and $\frac{1}{2}$ of the length. The lengths are measured as above and, for the calyx, from the point of insertion of the calyx tube to the tip of the longest lobe of the calyx.

(6) Inequality of the Calyx

In *G. amarella* the calyx-lobes are subequal or equal, while in *G. anglica*, *G. uliginosa* and *G. septentrionalis* they show varying degrees of inequality. The expression used is a

ratio of the lengths of the longest to the shortest calyx-arms, measured from their point of insertion on the calyx-tube.

(7) Seed size

In *G. amarella* and *G. septentrionalis* seed size varies between 0.5 and 1.2 mm. diameter.

Random samples of *G. amarella* were obtained only from a number of localities on the chalk of south-eastern England. These are comparatively homogeneous, and the various populations agree well in their general morphological appearance. A number of measurements were made; these confirmed this similarity. They are not reproduced in detail here, but were used as a standard with which to compare, in the first instance, existing herbarium material from other parts of the country. (Some of these chalk populations showed certain divergencies from the majority; these are discussed in a later paper on *G. germanica* and the hybrids *G. amarella* × *germanica*).

A large number of specimens of *G. amarella* from British herbaria was examined, and a number of measurements, subsequently expressed as outlined above, obtained. No clear differences could be seen, and it was necessary arbitrarily to divide the plants into four primary groups. The preliminary morphological examination, not specifically biometric, had revealed that there were certain general differences between the plants from the North of England and plants from the South. Because of this the preliminary grouping was on geographical criteria. Pigott (1954), working on the regional variation of *Thymus drucei* Ronn., has shown that this species can be divided into a number of "races", which are on the whole delimitable geographically. These geographical differences can be, at least partly, related to differences of habitat.

Working from this, the primary grouping was made as follows :

- Group I : S.E. & S.W. England & E. Anglia
v.cs. 1-34, 38.
- Group II : Wales & Welsh Border, Midlands
v.cs. 35-37, 39-58.
- Group III : Northern England
v.cs. 59-70.
- Group IV : Scottish Coastal
v.cs. 72-90, 102.

A few points of interest arise from the grouping of the data in this way.

- (1) The number of internodes in the plants of Group I is rather higher than that in the other groups, while that in Group III is the lowest.
- (2) In Group I the terminal internode is more commonly contracted than in Group III, although very similar to that of Group IV.
- (3) The ratio corolla length/calyx length is considerably higher in Group II, though there is an appreciable difference between Groups I & III.
- (4) The calyx teeth are more unequal in Groups III & IV than in the southern Groups.

These differences are not clear-cut, and in most instances their significance is low. In a series of t tests between Groups I & III, visually the most distinct groups, only the difference in number of internodes had a probability of less than 0.001, although the difference in the contraction of the terminal internodes showed a probability of less than 0.01.

Clearly some refinement of the grouping was required. As an approach to this, data for each plant were expressed as coloured symbols, plotted on an outline map. From the distribution of the symbols five secondary groups were examined, to which the sixth was later added. These were :

- (1) Chalk or oolite of S. England, as far north as Worcestershire, Warwickshire, Northamptonshire and S. Yorks. (v.cs. 3-38, 53, 54, 61 ; this group is essentially the same as group I above).
- (2) Dunes of N. Cornwall, N. Devon and S. Wales (and possibly coastal cliffs in the same areas) (v.cs. 1, 2, 4, 41, 44, 45.)
- (3) Dunes and small outcrops of carboniferous limestone in N. Wales and W. Lancashire (v.cs. 40, 49-52, 58-60, 69 ; this is substantially Group II above with the exclusion of the Pennine mass in Derbyshire).
- (4) Carboniferous and magnesian limestone in N. Midlands, N. and N.E. England (v.cs. 56, 57, 64-67, 69, 70).
- (5) Scottish dunes (& possibly some inland limestone in S. Scotland) (v.cs. 68, 82, 83, 85, 90, 91, 102).
- (6) Limestone and coastal dunes in Ireland (v.cs. H8, 10, 11, 13, 14, 16-19, 21-23, 25-28, 30, 33).

TABLE 1.
Statistical data for secondary groups 1-6 of *G. amarella*

CHARACTER	1		2		3		4		5		6	
	x	σ										
1. No. of Internodes	7.41	1.39	5.30	1.90	7.75	1.36	6.02	1.57	6.73	1.95	8.32	1.35
2. (Log A/T Int.) + 1	1.41	0.39	1.39	0.35	1.31	0.37	1.27	0.35	1.44	0.24	1.82	0.37
3. Leaf L/W	3.40	0.95	2.96	0.45	3.08	0.65	3.37	0.88	3.89	1.37	3.68	0.69
4. Leaf $\frac{B-A}{2L} \times 100$	7.80	3.00	9.00	2.72	8.88	2.42	7.84	2.75	7.36	3.66	6.94	1.97
5. Corolla length	1.70	0.20	1.72	0.10	1.70	0.22	1.71	0.22	1.69	0.14	1.94	0.20
6. Corolla/Calyx	1.63	0.26	1.56	0.24	1.64	0.26	1.56	0.26	1.45	0.20	1.71	0.21
7. Calyx longest/shortest	1.18	0.22	1.17	0.10	1.18	0.24	1.22	0.17	1.32	0.20	1.14	0.14

The means (\bar{x}) and standard deviations (σ) for each character and for these six groups are shown in Table 1. The results from this grouping are considerably more revealing. According to each of the characters measured the groups may be arranged in order of increasing magnitude of the mean values. This is done in Table 2 which shows also the probabilities obtained from t tests for each character and each pair of groups.

TABLE 2.

1 stop : probability > 0.05
 3 stops : „ < 0.05
 4 stops : „ < 0.01
 5 stops : „ < 0.001

Character	Order
No. of Internodes	2.4.5. . . . 1.3.6
(Log A/T Internode) + 1	4.3.2.1.5. . . . 6
Leaf L/W	2.3.4.1.6.5
Leaf $\left(\frac{B-A}{2L} \times 100\right)$	2.3.4.1.5.6
Corolla length	5. $\frac{1}{3}$.4.2. . . . 6
Corolla/Calyx	5. $\frac{2}{4}$.1.3.6
Calyx longest/shortest	5.4. $\frac{1}{3}$.2.6

The actual results of the *t* tests are not shown, but Table 3 shows the number of linkages out of 7 characters that each group shows. From Table 3 there is no evidence of a simple geographical cline. In most cases the differences between groups are fairly small, with the exception of those between group 6, the Irish plants, and the other groups. These are considered first.

TABLE 3.

No. of linkages	Groups covered (i.e. those in which $p > 0.05$)
0	4 & 6
1	2 & 6, 5 & 6
2	3 & 6
3	1 & 6
4	Nil
5	1 & 2, 1 & 4, 1 & 5, 2 & 3, 2 & 5, 3 & 4, 3 & 5
6	2 & 4, 4 & 5
7	1 & 3

Irish *G. amarella*

In 6 out of the 7 characters chosen, the Irish plants lie at one end of the scale. The exception is one of the leaf indices, and the differences in leaf shape throughout are not significant. Further, group 6 shows the greatest number of differences from other groups. These differences must be considered separately.

(1) Number of internodes. In group 6 the number of internodes is higher than in any other group. At the $p = 0.05$ level, it differs significantly from all other groups except Group 3. Its coefficient of variation ($C_V = 16.2\%$) is the least of all groups: (e.g. in group 3 $C_V = 17.5\%$, while in the homogeneous group 1 $C_V = 18.8\%$). (In the majority of the seven characters the coefficient of variation for group 6 is lower than that of the other groups. This agrees with the impression of uniformity gained in the preliminary examination of Irish plants.)

(2) (Log Average/Terminal Internode) + 1. If the constant in the formula is ignored, the value for the Irish plants is almost double that of group 5, the next highest. Its value of 1.82 indicates a ratio of terminal internode to average internode of about 0.17, which would be expected from the almost invariable suppression of the terminal internode in Irish plants. In other groups this suppression is frequent, but usually occurs in less than 50% of the individuals.

(3) and (4) Leaf-shape Indices. Although in these group 6 lies near the end of the scales, the differences are slight and not significant. However, in the second index the coefficient of variation is less than in other groups.

(5) Corolla Length. The distributions of corolla length for British, Irish and Continental material are shown in Figure 1. There is considerable overlap, but analysis reveals a very high degree of significance in the differences between British and Irish material. The Continental plants do not differ significantly from the British. The range of variation is lower in the Irish material, and on this character small gatherings of Irish material should be identifiable as such.

(6) Corolla/Calyx. This value is higher in the Irish plants, as would be expected, but the differences are slight and of little practical value.

(7) Calyx Longest/Shortest Lobes. The value for the Irish plants is the lowest, but again the differences are slight.

In the material which has been examined, the Irish plants form a homogeneous group,

which in several important characters lies outside the range of variation for British and European material.

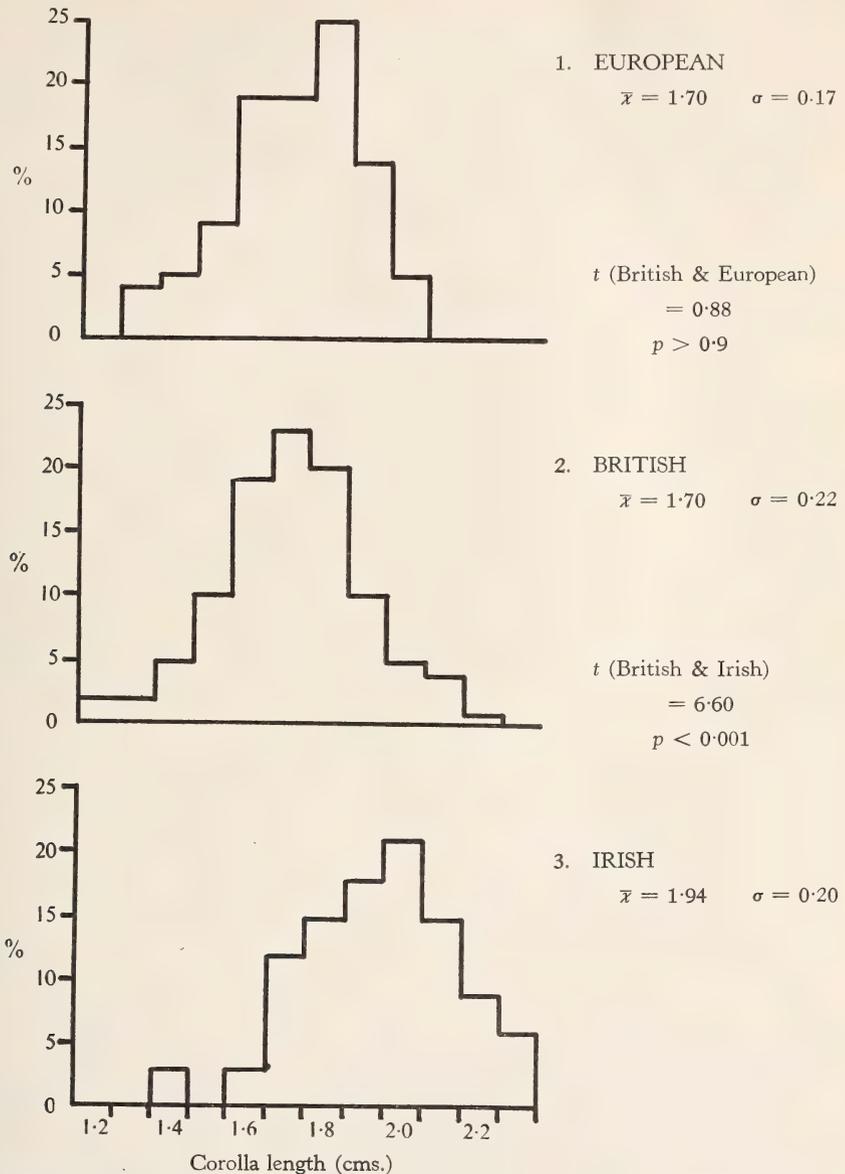


Fig. 1. Corolla lengths of British, Irish and European *G. amarella*.

Among the other five groups there are less obvious differences. The two major groups (1 & 4), those of Southern & Northern England, differ considerably in several characters, although there is no clear-cut distinction between them. They form the bulk of British *G. amarella*, and while they do not actually overlap geographically they can perhaps be regarded as forming a cline running from South Devon to Cumberland and Northumberland. Closely similar to group 1 are those plants found principally in the dune slacks of North Wales, Cheshire and Lancashire. This group is scarcely distinguishable from Group 1, but the few inland localities in which similar forms occur are limited to isolated patches of Carboniferous limestone in Shropshire, Denbighshire, Flintshire and

Caernarvonshire. For this reason, groups 1 & 3 must be regarded as geographically distinct.

Group 2 is extreme in a few characters, though again the differences are not great. The most noticeable are the small number of internodes, the rarity of suppression of the terminal internode and the broader, more tapering leaves. It is apparently restricted to the coastal cliffs and dunes of N. Cornwall, N. Devon and S. Wales, and thus lies outside the geographical ranges of the other groups.

Group 5 consists of those plants found in the dunes of E. Scotland and probably also of Islay and Colonsay. The corolla is smaller than that of other British plants, while the calyx is more usually and strongly unequal. The leaves are rather narrower than in the other groups. The group is geographically separate from Group 4, although a plant from Holy Island (v.c. 68) seems best placed with the Scottish dune plants, since its morphological and ecological affinities are with them rather than with the limestone forms.

In this way the heterogeneous and extremely variable taxon *G. amarella* can be divided into 6 groups, though some of these might be further divided. If the coefficients of variation are considered for various characters for the separate groups and for the whole lot of the plants, in most cases the variation of the total is greater than those of the groups making it up. This would be expected if the variation were not random throughout the country. In many cases the ranges of variation for the groups are similar, and since the standard deviation, and hence the coefficient of variation ($C_V = \frac{100 \times \text{standard dev.}}{\text{mean}}$), depends partly on the size of the groups, it would be expected to be less for the totals than for the necessarily smaller groups comprising those totals. Thus the actual differences of variation in the totals and the groups are probably larger than those indicated by the coefficients of variation.

TAXONOMIC CONCLUSIONS

Gentianella amarella (L.) Börner (1912)

Gentiana amarella L. (1753)

Hippion axillare Schmidt (1793)

Gentiana amarella subsp. *axillaris* (Schmidt) Murb. (1892)

Gentiana axillaris (Schmidt) Wettst. (1896)

From the work of Froelich (1796) onwards there has been confusion between *G. amarella* subsp. *axillaris* (Schmidt) and subsp. *lingulata* C.A. Agardh (= *G. axillaris* and *G. lingulata* as described by Wettstein (1896)). An examination of some European material of *G. lingulata* showed that it differed in a number of characters from *G. amarella*, especially leaf shape, number of internodes, geographical distribution and time of flowering, (i.e. substantially the differences described by Wettstein). This suggests that the two species of Wettstein's monograph should be retained. The name of *G. lingulata* thus becomes

Gentianella lingulata (C.A. Ag.) *comb. nov.*

Gentiana lingulata C.A. Agardh (1825)

Gentiana amarella subsp. *lingulata* (C.A. Ag.) Murb. (1892)

Gentiana lingulata (C.A. Ag.) Wettst. (1896).

According to both Wettstein and Murbeck, *G. lingulata* is represented in Britain only by var. *praecox* (Townsend) Wettst. This variety (= *Gentianella anglica* (Pugsley) E.F. Warb.) is discussed later. The common British plant (according to Wettstein) is *Gentiana axillaris* (Schmidt) Reichenbach.

The biometric investigation of British *G. amarella* reveals considerable regional

differentiation. The differences are easily distinguishable in small random samples, but are not large or sufficiently constant to warrant new names. It is therefore proposed to give them the title "races", this term having no nomenclatural significance. The Irish plants are different from all other British or European material of *G. amarella* in the size of their corollas, and this is correlated with other small but definite differences. It is proposed to raise this group to the rank of subspecies.

The specimen of *Gentiana amarella* in the Linnaean herbarium falls well within the range of variation of British plants (excluding Irish specimens). Since the specimen in *Hortus Cliffortianus* cited by Linnaeus (1753) is missing, the Linnaean Herbarium specimen is accepted as the type of *G. amarella* Linnaeus. Pugsley (1936) remarks that in the Linnaean Herbarium there is also a sheet of *G. germanica* (Willd.) Börner, and he rejects the name *G. amarella* in favour of *G. axillaris* (Schmidt) Rchb. Since, however, the Linnaean sheet of *G. amarella* bears the number 17 in Linnaeus' own handwriting (Savage, 1945) this can be accepted as unambiguous, and Pugsley's suggestion ignored.

Linnaeus' type is also automatically the type specimen of the following subsp. *Gentianella amarella* subsp. *amarella*. Biennial. Stem 3-50 cm. high, of 4-9 (-10) internodes. Internodes \pm equal, or else the terminal one reduced to about 1 mm. Basal leaves of first year lanceolate to lingulate, of second year obovate or spatulate. Stem leaves lanceolate to ovate-lanceolate, \pm acute. Flowers pentamerous or tetramerous, sometimes both on one plant. Calyx teeth subequal to markedly unequal, 0.5 - 0.8 of the length of the corolla. Corolla (1.4 -) 1.6 - 1.8 (-2.0) cm. long, dull blue purple. Flowers from (late July -) August-September.

In Great Britain it can be divided into the five following races :

(I) Southern Chalk and Limestone Race

Plant 3-50 cm. high, of (5 -) 6 - 9 internodes. Terminal internode contracted in the majority of plants, so that the topmost 2 pairs of leaves are more or less contiguous. Terminal pedicel about equal to the internodes. Stem leaves ovate-lanceolate—lanceolate, more or less acute. Calyx teeth subequal (equal in about one-third of the plants), corolla 1.5-1.8 times the length of the calyx. [Seeds 0.8-0.9 mm. diameter.] Distribution : Chalk, oolite and carboniferous limestone in South and South-east England and South Midlands from South Devon and Kent to Shropshire and Lincolnshire.

Vice-comital distribution : 3, 5-25, 28-38, 40, 53, 54, 61.

(II) Bristol Channel Race

Plant usually 5-15 cm. high, of (2 -) 3-7 internodes. Terminal internode usually not markedly contracted, more or less equal to the others. Terminal pedicel equalling or slightly exceeding the internodes in length. Leaves ovate-lanceolate, even ovate, more or less acute, tapering sharply from the slightly widened base. Corolla 1.25-1.7 times the length of calyx teeth. Calyx teeth markedly unequal in most specimens. [Seeds 0.7-0.9 mm. diameter.]

Distribution : Sand-dunes and coastal cliffs on Culm measures and Old Red Sandstone in North Cornwall, North Devon and South Wales. Vice-comital distribution : 1, 2, 4, 41, 44, 45.

(III) North Wales and Lancashire Coastal Race

Scarcely distinguishable from the Southern Chalk and Limestone Race, and perhaps identical with it, but separated because of discontinuity and difference in habitat.

Distribution : Sand dunes and more or less coastal limestone from North Wales to Lancashire. Possibly inland in Shropshire. Vice-comital distribution : (40), 49-52, 58-60, 69.

(IV) Northern Limestone Race

Plants usually rather smaller than in Race I, from 5-30 cm., of 4-7 internodes. Terminal internode usually not markedly contracted, although it is in a few plants. Terminal pedicel more or less equalling the internodes. Leaves lanceolate to ovate-lanceolate, \pm acute, except for the uppermost which are often sub-obtuse. Corolla usually about 1.5 times as long as the calyx-teeth. Calyx-teeth markedly unequal. [Seeds 0.8-0.9 mm. diameter.]

Distribution : Carboniferous and Magnesian Limestone pastures and coastal cliffs from Stafford and Derby to Cumberland and Northumberland.

Vice-comital distribution : 39, 56, 57, 60, 62-67, 69, 70.

(V) Scottish Coastal Race.

Plants normally 10-50 cm. high, of (5 -) 6-10 internodes. Terminal internode normally strongly contracted. Terminal pedicel more or less equalling the internodes. Leaves lanceolate, more or less acute. Corolla 1.25-1.5 times as long as the calyx teeth. Calyx teeth markedly unequal. [Seeds ca. 0.7 mm. diameter.]

Distribution : Coastal dunes of Islay, Colonsay and of Northumberland and East Scotland from Holy Island to Fife and Forfar.

Vice-comital distribution : 68, 82, 83, 85, 90, 102.

The total vice-comital distribution of *G. amarella* subsp. *amarella* is this : 1-17, 19-25, 28-42, 44, 45, 49-70, 82, 83, 85, 90, 102. Druce (1932) quotes in addition 47, 48, 80, 81, 86, [88, 89, 92-95], 97, 100, [105-112]. Of these, those enclosed in square brackets clearly represent *G. septentrionalis*. I have seen no plants from the remaining 10 vice-counties, and can therefore neither confirm nor reject the records.

GENTIANELLA AMARELLA subsp. *hibernica*, subsp. nov. (Plate 12).

For the reasons already discussed, it is proposed to describe the Irish race of *G. amarella* as a new subspecies.

The plant differs from *G. amarella* subsp. *amarella* in its unusually large corolla of (1.7 -) 1.9-2.2 cm., which is reflected in the corolla-calyx ratio of 1.5-1.8 (- 2.0). The calyx teeth are subequal. The number of internodes is rather higher (7-11) and the terminal one is almost always very markedly contracted. The leaves are less tapering than those of subsp. *amarella*, and linear-lanceolate, acute or subacute.

Differt a *G. amarella* subsp. *amarella* : Internodia 7-11, summum semper maxime contractum (ad ca. 1 mm. longum). Folia caulina media et superiora lineari-lanceolata vel lanceolata, acuta vel acutiuscula. Corolla (1.7 -) 1.9-2.2 cm. longa, quam calycis laciniae 1.5-1.8 (- 2.0) -plo longior.

Habitat in pascuis calcareis Hiberniae.

Holotypus in Herb. Mus. Nat. Hibern. (Dublin) : South of Laytown, Co. Meath, *R. Ll. Praeger*, Aug. 1895.

The vice-comital distribution of the specimens seen is H8, 10, 13, 14, 17-19, 21-23, 25-28, 30, 33.

Gentianella anglica

G. anglica appears to be endemic to England, although it was well known to Murbeck and Wettstein, who regarded it as a variety of *G. lingulata*. It is considerably less variable than *G. amarella*, forming (with one exception) a clearly defined taxon occupying a rather limited geographical area.

It differs from *G. amarella* in a number of ways, and, to examine the value of these,

PLATE 12.



H7

G. amarella subsp. *hibernica* : Laytown, C. Meath, Eire.



measurements were made of the plants from three random samples collected in Surrey, Lincolnshire and Berkshire. A summary of the statistical data for these, compared with two chalk populations of *G. amarella* and herbarium material of European *G. lingulata* appears in Table 4. (The measurements of *G. lingulata* are from exsiccata cited by Wettstein (1896)).

TABLE 4.
Statistics of *G. anglica*, *G. amarella* and *G. lingulata*

Character	<i>G. amarella</i>				<i>G. anglica</i>						<i>G. lingulata</i>	
	Oxon.		Surrey		Surrey		Lincs.		Berks.		Europe	
	x	σ	x	σ	x	σ	x	σ	x	σ	x	σ
1. No. of Internodes	6.41	1.11	6.89	1.07	1.97	0.61	2.89	0.74	2.30	0.53	4.69	1.00
2. (Log A/T Int.) + 1	1.60	0.40	1.57	0.39	0.78	0.11	0.94	0.15	0.82	0.12	1.69	0.72
3. Log Ht/T. Ped.	0.89	0.24	0.90	0.25	0.14	0.33	0.37	0.27	0.13	0.27	0.78	0.35
4. Leaf L/W	3.11	1.28	2.85	0.61	3.75	1.05	4.25	0.93	4.28	1.45	4.00	0.39
5. Leaf $\frac{B-A}{2L} \times 100$	7.95	3.44	7.19	2.23	3.30	3.13	3.50	2.63	1.27	4.58	0.77	1.42
6. Corolla length	1.64	0.19	1.60	0.16	1.55	0.15	1.67	0.12	1.44	0.20	1.79	0.15
7. Corolla/Calyx	1.71	0.23	1.56	0.19	1.51	0.13	1.47	0.22	1.45	0.21	1.39	0.14
8. Calyx longest/shortest	1.10	0.13	1.10	0.15	1.48	0.23	1.25	0.20	1.27	1.17	1.14	0.08

Within the three random samples of *G. anglica* there is generally close agreement. The average heights of the plants in each population are much the same (430, height = 7.6 cm.; 434, height = 8.0 cm.; 437, height = 7.7 cm.). The differences between them are in some cases considerable (e.g. in number of internodes, the difference between the means of 430 and 434 has a probability of less than 0.001), but none of the samples can be clearly separated from the other two, nor any two of them be completely united. Thus, 430 agrees with 437 in the relative length of the terminal internode, and with 434 in the taper of the leaf, while 434 and 437 agree in the ratio of leaf length/breadth, and in the inequality of the calyx-teeth. All three agree closely in the ratio of corolla length/calyx length. In 437, the leaves tend to be more lingulate, while 434 has an unusually large corolla and in 430 the inequality of the calyx-teeth is very marked. Many more differences could be described, but none of them is sufficiently marked to enable one with certainty to place any individual plant definitely in one sample rather than another.

By comparison with *G. amarella*, the three samples are alike in their marked differences from that species. These are described separately, together with supplementary data not recorded in the table. The characters discussed are those which either do or have been supposed to separate the species.

(1) Smaller and more branched (Townsend). The average height of *G. amarella* is between 12 and 15 cm., that of *G. anglica* about 8 cm., though these measurements are extremely dependent on the habitat. *G. amarella* ranges from 2-40 cm., *G. anglica* from 2-20 cm. *G. anglica* is normally branched from the base, with long, leafy flowering branches, often giving the plant a more or less pyramidal appearance, though often simple. *G. amarella* usually bears short branches from most of the leaf-axils, though again this factor is dependent on the environment. *G. lingulata* resembles *G. amarella* in its branching, but the number of internodes is more or less intermediate between that species and *G. anglica*.

(2) Leaves narrower, the lower ones rounded at the apex (Townsend). No direct calculations from leaf width were made, as this depends very much on the size of the plant. So far as the length/width ratio is concerned, this tends to be higher for *G. anglica*, though

the overlap is great. In addition, the Scottish plants (for example) of *G. amarella* tend to have a low length/width ratio. The differences between the taper of the leaves is more marked, giving a ratio of $\left(\frac{B-A}{2L} \times 100\right)$ of up to 7 times as great in *G. amarella*. This feature is very obvious in the field; although the upper leaves of *G. anglica* often show a marked taper, they lack the expanded base so often found in *G. amarella*. The lower leaves, and especially those forming the basal rosette, are generally obtuse in *G. anglica*, although their shape cannot usually be described as lingulate. In *G. lingulata* taper is frequently lacking, a fact revealed by the very low value in Table 4 for this species.

(3) Flowers mostly long-stalked (Townsend). In *G. anglica* the terminal pedicel represents about 0.4-0.5 of the total height of the plant. In *G. amarella* the average value is only about 0.1. For *G. lingulata* the value is about 0.3.

(4) Flowering about May (Townsend). The earliest recorded date of flowering for *G. anglica* is 26 March (Cornwall), while the latest I have seen is 12 July (Berkshire); at this latter date all the plants were more or less in fruit. For *G. amarella* in Britain, the earliest date I have met is 22 July (Glamorgan), the latest 29 September. For the specimens of *G. lingulata* examined, the earliest date was 12 July (Poland), and the latest 8 August (Hungary). For this last species Wettstein gives the flowering dates as May to the middle of July, or later in the North. Wettstein does not further amplify his statements but it seems at least possible that his dates include *G. anglica* (his *G. lingulata* var. *praecox*) as I have seen no specimens of *G. lingulata* flowering in May or June.

(5) Internodes 2-4 in number (Murbeck). The mean value for *G. anglica* is 2.31, for *G. lingulata* 4.69 and for *G. amarella* 6.65.

(6) Calyx teeth scarcely as long as the tube (Murbeck). The average tube length in both *G. anglica* and *G. amarella* is 0.40 cm. The tooth length in *G. amarella* (ca. 0.7 cm.) is slightly shorter than that in *G. anglica* (ca. 0.8 cm.), and the difference might be held to agree with Murbeck's description. No obvious difference exists between *G. amarella* and *G. lingulata*.

(7) Terminal internode longer than the others. In *G. anglica* the average length of the terminal internode is 1.5 times that of the average internode length. In *G. amarella* the value is about 0.3 and in *G. lingulata* about 0.2. Thus the suppression more or less marked in both *G. amarella* and *G. lingulata* is absent altogether, and replaced by an elongation of the terminal internode.

(8) Calyx teeth more unequal. In the samples of *G. amarella* 50% of the plants had equal calyx-teeth. In *G. anglica* only 8% of the plants had equal calyx-teeth, and in *G. lingulata* 15%.

From these facts, *G. anglica* must be regarded as quite distinct from *G. amarella* and *G. lingulata*, although showing a closer morphological resemblance to the latter. In its habit, its time of flowering and its geographical distribution, it is also quite distinct.

THE CORNISH *G. anglica*

Except in North Cornwall and North Devon, *G. anglica* is restricted completely to chalk grassland. An examination was therefore made of a small number of plants from these counties. Those from N. Devon (Braunton Burrows) are in all respects similar to the Eastern plant. The data for those from Cornwall, where the plant is found on coastal cliffs in short turf, are compared in Table 5 with average values for the three populations of *G. anglica* already described.

The flowering dates of the Cornish plants vary from 26 March to 26 June, and July (date unspecified). They are thus more or less the same as those of *G. anglica* on the chalk.

TABLE 5.
Eastern and Cornish *G. anglica*, and *G. lingulata*

Character	430, 434 & 437		Cornish		<i>lingulata</i>	
	\bar{x}	σ	\bar{x}	σ	\bar{x}	σ
1. No. of Internodes	2.31	0.71	3.88	0.60	4.69	1.00
2. (Log A/T internode) + 1	0.83	0.14	0.06	0.40	1.69	0.72
3. Log Ht/T. pedicel	0.19	0.31	0.30	0.16	0.78	0.35
4. Leaf L/W	4.07	1.22	3.75	0.75	4.00	0.39
5. Leaf $\frac{B-A}{2L} \times 100$	2.57	3.80	3.63	2.64	0.77	1.42
6. Corolla length	1.54	0.19	1.77	0.22	1.79	0.15
7. Corolla/Calyx	1.47	0.19	1.44	0.12	1.39	0.14
8. Calyx longest/shortest	1.35	0.23	1.13	0.10	1.14	0.08

There are certain striking distinctions from chalk *G. anglica*. The average number of internodes is considerably higher, and more like that of *G. lingulata*. The terminal internode is slightly contracted instead of elongated (about 0.8 the average length). The corolla is longer than that of any other British members of the *G. amarella* aggregate except for Irish *G. amarella*, and more closely similar to that of *G. lingulata*. In addition, the habit of Cornish *G. anglica* is rather more like that of *G. amarella* than *G. anglica*, since it usually bears axillary flowers and is seldom branched from the base. The basal leaves are broadly spatulate.

Taking all these characters into consideration, the position of the Cornish plants seems to be somewhat intermediate between *G. anglica* and *G. amarella*, though rather closer to the former.

Over the total range of *G. anglica*, if Cornwall is excluded, there is a general cline in the direction of S.W.-N.E., from South Devon to Lincolnshire. This is most marked in the number of internodes and the corolla length, both of which increase roughly from S.W. to N.E. The cline cannot be shown exactly, and there are many exceptions, but it nevertheless bridges the gaps between the three random samples quite neatly.

TAXONOMIC CONCLUSIONS

Gentianella anglica (Pugsley) E. F. Warb. (1952)

Gentiana amarella var. γ *praecox* Townsend (1883)

Gentiana lingulata var. *praecox* (Townsend) Wettst. (1896)

Gentiana anglica Pugsley (1936)

The resemblances of *G. anglica* to *G. amarella* and *G. lingulata* are slight, and *G. anglica* is retained as a species. The similarity to *G. lingulata* is restricted to the lingulate lower leaves, a condition found also in some forms of *G. septentrionalis*. The geographical range of *G. anglica* lies entirely within that of *G. amarella* and apparently little or no hybridisation occurs. This is probably owing to the difference in flowering time, but the subject requires experimental investigation.

In the original description, Townsend (1883) says that attention was first drawn to the plant by Stratton in 1878. Townsend had received specimens from Stratton, gathered 27 May 1878, from the downs above Steephill, Isle of Wight. The specimens in Townsend's herbarium have not been seen, but there are in Herb. Univ. Oxon. two sheets both labelled "Chalkdown, Steephill, 27 May 1878" and both ex Herb. F. Stratton. These are thus isotypes, and they agree well with the greater number of British specimens. Townsend's description is quoted :

" *G. Amarella* var. *γ praecox*.

Var. *γ praecox* is a smaller and more branched plant than the type; in height it seldom exceeds three inches; the leaves are narrower, the lower ones rounded at the end; the flowers are mostly long-stalked. The corolla is more usually 4-cleft; the corolla and calyx segments are apparently broader in proportion to their length, and the filaments broader and inserted higher in the tube. It flowers about May."

From the examination of the Cornish plants of *G. anglica*, it is evident that these differ from Townsend's plant in several particulars. They show a tendency towards *G. lingulata*, but their resemblances are still rather with *G. anglica* than with the former species. Because of their morphological differences, the ecological differences and the wide break in geographical distribution on the one hand, and because of the general morphological similarities in some characters and the similar flowering time, it is proposed to describe these Cornish plants as a subspecies of *G. anglica*.

Townsend's plant thus becomes :

Gentianella anglica (Pugs.) E. F. Warb. subsp. *anglica*.

Plant 4-20 cm. high, of 2-3 (- 4) internodes. Terminal internode about $1\frac{1}{2}$ times as long as the average, occasionally contracted, when the second one is much expanded. Terminal pedicel forming about $\frac{1}{2}$ the height of the plant, frequently even more. Basal leaves narrowly spatulate, obtuse. Middle and upper stem leaves lanceolate, acute, lower ones sometimes more or less linear, obtuse or sub-obtuse. Corolla 1.3-1.6 cm. long, about $1\frac{1}{2}$ times as long as the calyx-teeth. Calyx-teeth markedly unequal. Flowers from (April -) May-June (- July).

While the Cornish plants are :

Gentianella anglica subsp. **cornubiensis** subsp. nov. (Plate 13).

This differs from subsp. *anglica* thus : Plant 4-15 cm. high, of 3-5 internodes. All internodes more or less equal in length. Terminal pedicel rather larger than the internodes, but less than $\frac{1}{3}$ of the height of the plant. Basal leaves broadly spatulate or rosulate, obtuse. All stem leaves linear to linear-lanceolate, obtuse or subobtuse, the uppermost occasionally somewhat acute. Corolla (1.5 -) 1.7-2.0 cm. long, about $1\frac{1}{2}$ times as long as the calyx-teeth. Calyx-teeth subequal. Flowers (March -) April (- July).

Differt a subsp. *anglica* : Planta 4-15 cm. alta, a 3-5 internodiis constructa. Internodia omnia plus minus aequalia. Pedicellus floris terminalis quam internodia paullum longior, sed partem tertiam plantae totae non aequans vel superans. Folia basalia late spatulata vel rosulata, obtusa. Caulina linearia vel lineari-lanceolata, obtusa vel obtusiuscula, summa rarius subacuta. Corolla (1.5 -) 1.7-2.0 cm. longa, quam calycis laciniae $1\frac{1}{2}$ -plo longior. Calycis laciniae subaequales.

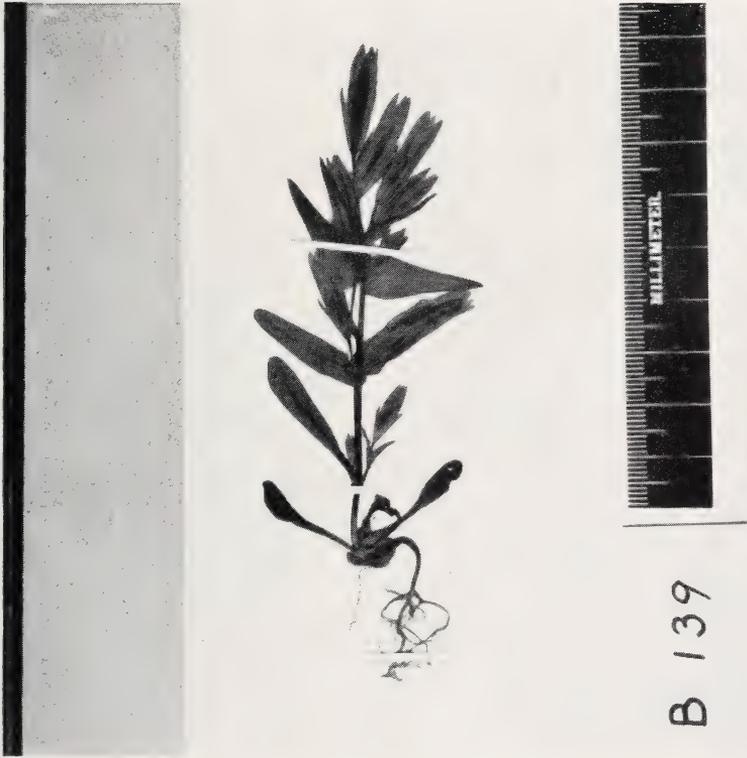
Holotypus in Herb. Mus. Brit. Penhale, Perranzabuloe, Cornwall. 26 March 1907. J. F. P. coll. et comm. ad F. Hamilton Davey.

Distribution :

(I) *G. anglica* subsp. *anglica*. Chalk grassland from S. Devon and Dorset to Lincolnshire. Formerly on dunes at Braunton Burrows, N. Devon, now believed extinct. V.cs. 3, 4, 6-11, 13, 17, 22, 24, 30, 32, 53.

(II) *G. anglica* subsp. *cornubiensis*. Coastal cliffs in W. Cornwall, v.c. 1.

PLATE 13.



G. anglica subsp. *cornubiensis* : Perranzabuloe, Cornwall.



Gentianella uliginosa

G. uliginosa was the first segregate of Linnaeus' *G. amarella* to be recognised as distinct (Willdenow, 1797). According to Murbeck and Wettstein it was to be regarded as the annual analogue of *G. amarella*, but it was retained as a species. Its duration has already been dealt with.

The early history of *G. uliginosa* in Britain is somewhat chequered. According to Druce (1932) it occurred in v.cs. 45, Pembroke, and 107, Sutherland. Wettstein (1896) quotes v.cs. 57, Derby; 65, N.W. Yorks; 90, Forfar. Marshall (1899) recorded the plant from Nairn (v.c. 96). The first correct record in Britain appears to be that of Pugsley (1924) from Tenby, Pembrokeshire.

In a note on the plant's habitats and distribution, Lousley (1950) considered all these records and disposed of them, except for Pugsley's Tenby record (v.c. 45), and in addition added records from v.c. 41, Glamorgan. In Britain the plant appears restricted to dune slacks in South Wales.

At various times, the differences between *G. uliginosa* and *G. amarella* have been described. In the following discussion, numbers 1 and 2 are from Willdenow's original description, 3-6 from Murbeck's comments (1896) and the remainder from my own observations.

In order to examine these differences, measurements were made of Continental *G. uliginosa*, cited by Murbeck, and of three random samples from South Wales.

These were:

438 : Oxwich Burrows, Glamorgan, 1955

518 : Same locality, 1956

519 : 400 yards east of above.

Plants from other localities in v.c. 41 were not included, as I suspected hybridisation with *G. amarella*.

The statistical data for these plants are shown in table 6 where measurements for *G. amarella* are also included. (These last are average values for all southern *G. amarella* (group 1) and all Bristol Channel *G. amarella* (group 2).)

TABLE 6.
Statistical data for *G. amarella* and *G. uliginosa*

Character	<i>amarella</i> group 1		<i>amarella</i> group 2		438		518		519		Continental <i>uliginosa</i>	
	x	σ	x	σ	x	σ	x	σ	x	σ	x	σ
1. No. of Internodes	7.41	1.39	5.30	1.90	1.64	0.48	1.61	0.76	1.36	0.48	4.13	0.91
2. (Log A/T Int.) + 1	1.41	0.41	1.39	0.35	0.75	0.06	0.80	0.03	0.78	0.08	1.06	0.46
3. Log Ht/T. Pedicel	0.99	0.27	0.79	0.35	1.79	0.41	1.72	0.47	1.69	0.36	0.61	0.35
4. Leaf L/W	3.40	0.91	2.96	0.45	2.89	0.66	3.42	0.72	3.36	0.71	3.16	0.84
5. Leaf $\frac{B-A}{2L} \times 100$	7.80	2.99	9.00	2.72	8.14	2.70	4.72	2.40	5.82	2.16	8.81	4.84
6. Corolla length	1.70	0.20	1.72	0.10	1.46	0.29	1.56	0.20	1.61	0.26	1.49	0.14
7. Corolla/Calyx	1.63	0.28	1.56	0.24	0.99	0.14	1.43	0.17	1.43	0.25	1.12	0.10
8. Calyx longest/shortest	1.18	0.20	1.17	0.10	1.14	0.12	1.21	0.16	1.32	0.39	1.16	0.14

The following features emerge from the table, and from my own field-observations.

(1) Stem always more branched and slightly winged at the base. The complicated life-history of *G. uliginosa* has been noted. The larger plants, i.e. the biennials and possibly some long-season annuals, are slightly winged at the base, though this does not seem to be a very marked character nor a constant one. The larger plants also invariably have branches from the base of the plant, these branches being long and bearing 1 (– 2) flowers. This gives the whole plant a distinctly pyramidal habit, quite different from that of any form of *G. amarella*, and distinct even from *G. anglica*. (The Continental material of *G. uliginosa* examined does not show this character.)

(2) Flower colour. Willdenow describes the flowers of *G. uliginosa* as “caerulescens,” but gives no colour for *G. amarella*. No clear difference has been noted in the field, but direct comparison with *G. amarella* has not been made. The colour of British *G. uliginosa* is the usual bluish-purple of *G. amarella*.

(3) Annuals. This character has been dealt with already.

(4) Basal leaves ovate or lanceolate. This is in general true, but there is frequently a distinct tendency towards oblanceolate or even spatulate. This may be related to annual/biennial duration as in the 1st and 2nd year rosettes of *G. amarella*. In any case, this character will not serve to separate the two species.

(5) Calyx teeth very unequal. In 518 and 519 the values for calyx longest/shortest teeth are higher than those for *G. amarella*, though lower than in *G. anglica*. In 438, from the same population as 518, they are not. (See 6 below.)

(6) Corolla tube equal to or shorter than calyx. In 438 the corolla length (to tip of teeth) is more or less equal to the calyx (corolla/calyx = 0.99). In 518 and 519 the values are less than in *G. amarella*, but still high (1.43 in both). The corolla-tube in these, however, but slightly exceeds the calyx.

While the results of measurements in characters (5) and (6) are somewhat opposed, the flowers of *G. uliginosa* have a different appearance from those of *G. amarella* or *G. anglica*. The calyx teeth are broader and altogether larger, and more spreading. These characters are evident also in the continental specimens of *G. uliginosa*, and form together one of the most obvious differences between the two species.

(7) Middle stem leaves broader at the base. Again 438 is distinct from 518 and 519. In 438 the value for leaf L/W is lower, and lower also than in chalk *G. amarella*, though not than Bristol Channel *G. amarella*. Between 518/519 and chalk *G. amarella* there is no difference, while Continental *G. uliginosa* is intermediate. In the leaf-taper index, 518 and 519 show leaves less tapered than *G. amarella*, while these latter are similar to 438 and continental *G. uliginosa*.

Thus, in flower and leaf characters there are considerable discrepancies between the samples of *G. uliginosa*. A possible explanation for some of these discrepancies is considered below, in the section on hybridisation between *G. amarella* and *G. uliginosa*.

(8) Terminal pedicel much elongated, frequently as long as the stem. In *G. amarella*, the terminal pedicel is about 0.12 of the total height of the plant. In all the samples of *G. uliginosa* it is about 0.7 of the total height, or about 1.8 times as long as the height from basal rosette to the topmost node. The difference is even more marked than that between *G. amarella* and *G. anglica*.

(9) Terminal internode somewhat elongated. In *G. amarella* the terminal internode is about 0.4 of the average length. In *G. uliginosa* it is about 1.7 times the average. (The elongation of terminal pedicel and terminal internode are closely correlated throughout the *G. amarella* aggregate, and serve to distinguish *G. uliginosa* and *G. anglica* from the other members with almost complete certainty.) In Continental *G. uliginosa* the value for terminal pedicel/height to top node is 0.25 (0.20 of total height) and that for terminal

TABLE 7.

Statistical data for *G. amarella*, *G. uliginosa* and putative hybrids

CHARACTER	<i>amarella</i>			519A		
	Range	\bar{x}	σ	Range	\bar{x}	σ
1. No. of Internodes	3 - 10	7.41	1.39	1 - 8	4.00	2.27
2. (Log A/T Int.) + 1	0.7-2.2	1.41	0.41	0.7-1.4	0.96	0.23
3. Log (Ht/T. Ped.)	0.3-2.0	0.99	0.27	$\bar{2}$.7-1.2	0.39	0.62
4. Leaf L/W	1.5-7.0	3.40	0.91	3.0-6.0	4.00	0.90
5. Leaf $\frac{B-A}{2L} \times 100$	0 - 17	7.80	2.99	0 - 10	5.75	2.54
6. Corolla length	1.2-2.1	1.70	0.20	1.4-1.9	1.64	0.17
7. Corolla/Calyx	1.0-2.3	1.63	0.28	1.1-2.1	1.60	0.27
8. Calyx long./short.	1.0-2.0	1.18	0.20	1.0-1.2	1.07	0.08

CHARACTER	520			<i>uliginosa</i>		
	Range	\bar{x}	σ	Range	\bar{x}	σ
1. No. of Internodes	2 - 9	5.47	2.16	1 - 3	1.57	0.62
2. (Log A/T Int.) + 1	0.7-1.5	1.04	0.19	0.7-1.0	0.78	0.06
3. Log (Ht/T. Ped.)	$\bar{1}$.9-1.0	0.61	0.32	$\bar{2}$.8-0.6	$\bar{1}$.73	0.42
4. Leaf L/W	2.0-3.5	2.93	0.41	2.0-4.5	3.23	0.73
5. Leaf $\frac{B-A}{2L} \times 100$	0 - 9	5.40	2.70	0 - 12	6.16	2.84
6. Corolla length	1.1-1.9	1.69	0.22	0.9-2.2	1.55	0.27
7. Corolla/Calyx	1.4-3.6	1.85	0.52	0.8-2.0	1.29	0.27
8. Calyx long./short.	1.0-1.5	1.19	0.18	1.0-2.5	1.22	0.24

internode/average internode 0.87. These values are intermediate between those for British *G. amarella* and *G. uliginosa*.

(10) Number of internodes 1-3. The average value for British *G. uliginosa* is 1.56 internodes, and for British *G. amarella* about 6.5 internodes. There is no overlap. In continental *G. uliginosa* the value (4.13) is intermediate.

In Britain, there are several points of distinction between the two species which are clear-cut, and there is no difficulty in separating them. However, an examination of natural populations in the field suggested a certain degree of intermediacy in some populations, and these were sampled and tested for the possibility of hybridisation.

HYBRIDS BETWEEN *G. amarella* AND *G. uliginosa*

Two putative hybrid populations were sampled and examined; these were :

519a : 25 yards from 519 (pure *G. uliginosa*)

520: Whiteford Burrows, Glamorgan.

The statistical data for these two populations, for an "aggregate" of populations 438, 518 and 519 (*G. uliginosa*) and an aggregate of *G. amarella* (all British plants) are set out in Table 7.

From this table it is seen that in number of internodes, contraction or otherwise of terminal internode and terminal pedicel, and corolla length the putative hybrid populations are intermediate between *G. amarella* and *G. uliginosa*, while the ranges of these characters also overlap those of the pure species. Figures 2-4 show these ranges. (In these histograms populations 519a and 520 are combined.) The histograms show that the range of variation (summarised by the standard deviations and standard errors of the means) is greater for each character in the hybrid populations than in the pure populations.

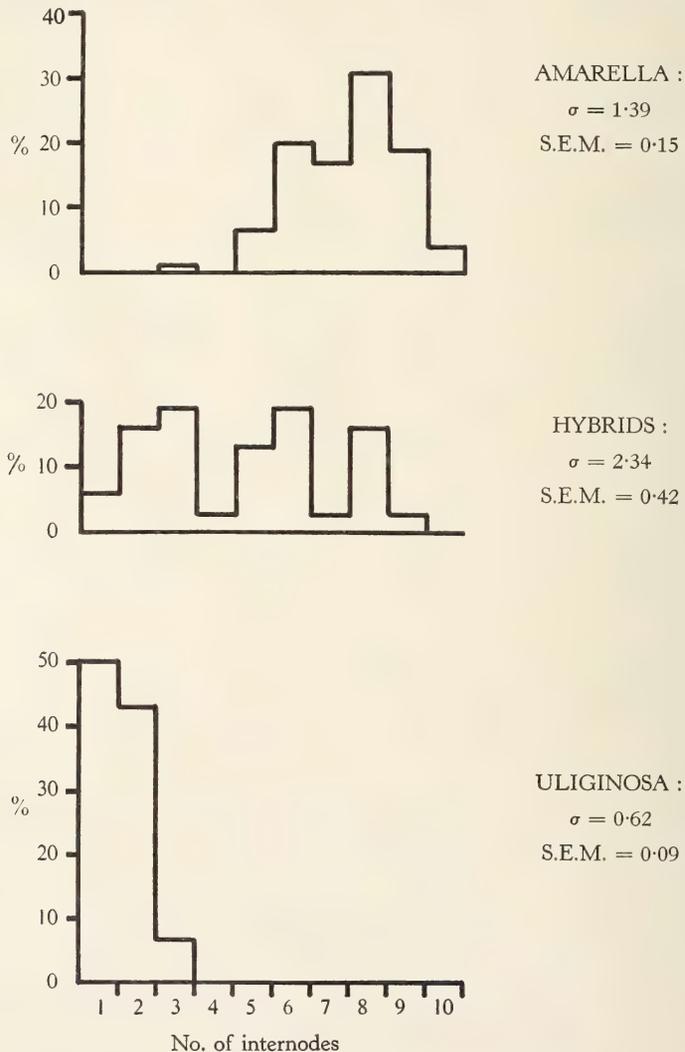


Fig. 2. *G. amarella*, *G. uliginosa* and hybrids : no. of internodes.

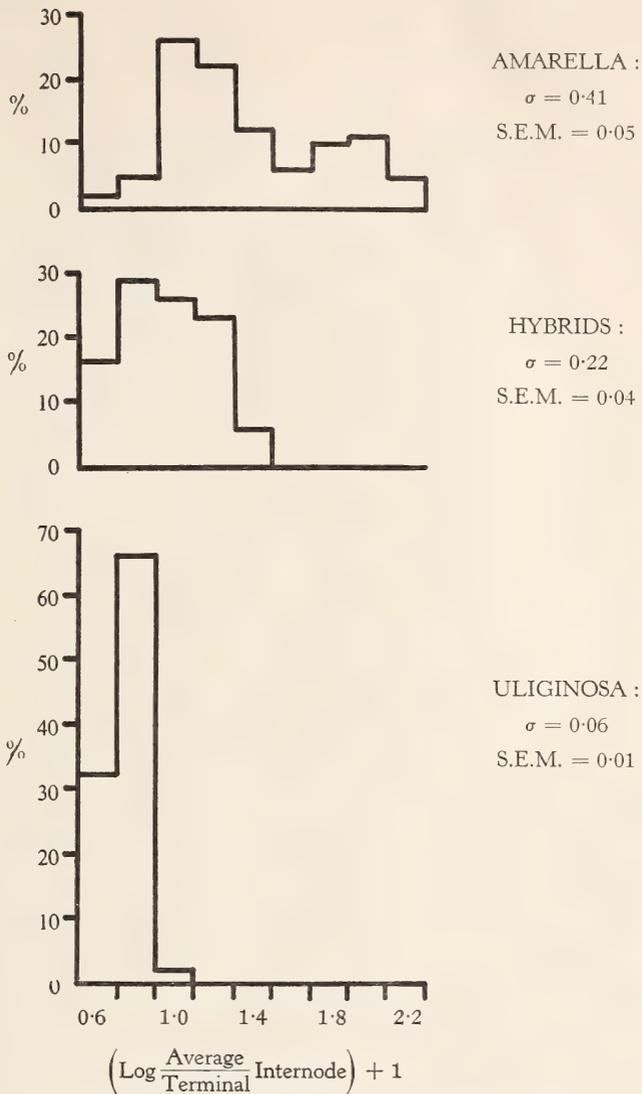


Fig. 3. *G. amarella*, *G. uliginosa* and hybrids: relation between terminal and average internode lengths.

A further investigation was made, in which pollen grains from 2 anthers on each of 5 plants were examined. In each case 10 pollen grains were examined from each anther. The results are shown in table 8.

The sampling of pollen was not made in a random way. An anther was crushed on a slide, and the first 10 pollen grains within an eyepiece field examined. The results are nevertheless suggestive of hybrid origin for population 519a. Apparently *G. uliginosa* and

TABLE 8.

Population	% good pollen
amarella : 521; Kenfig, Glamorgan	95.0 ± 06.7
Hybrids : 519a; Oxwich Burrows	70.0 ± 12.7
uliginosa : 438; Oxwich Burrows	89.0 ± 07.0

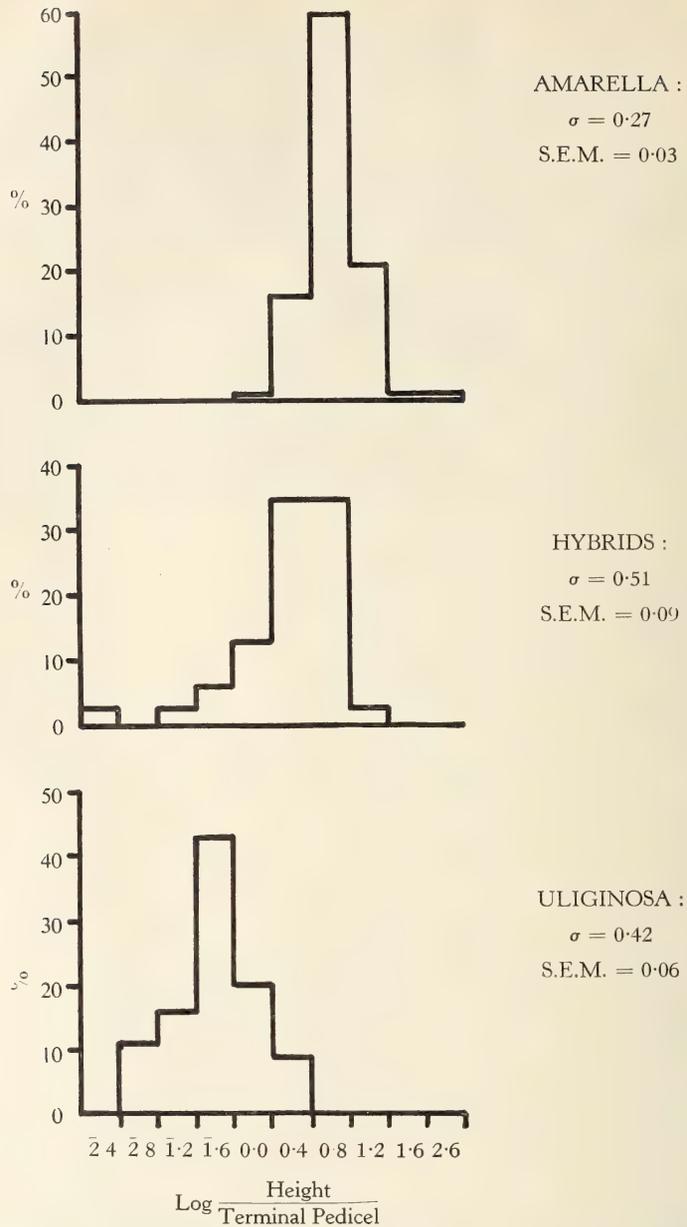
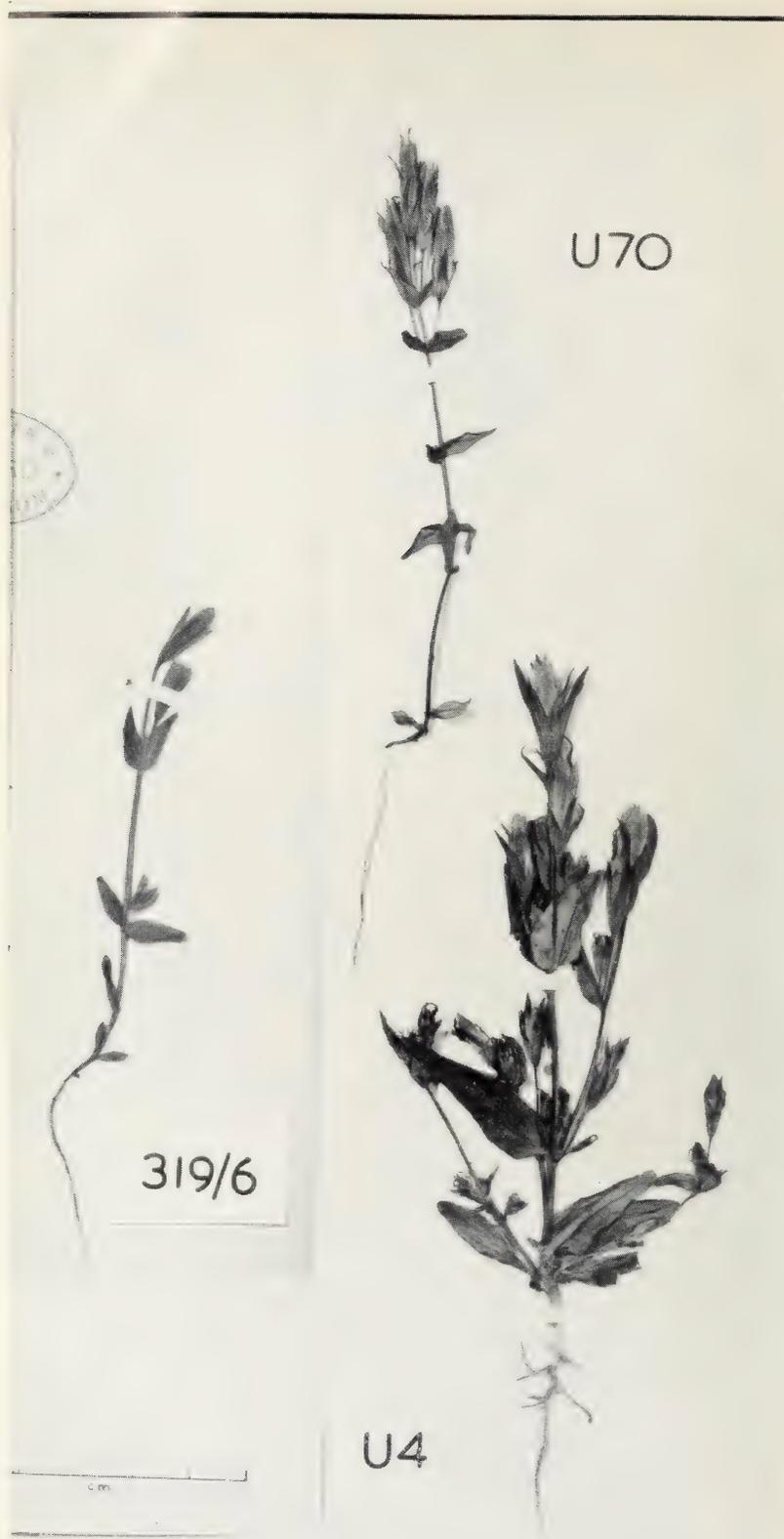


Fig. 4. *G. amarella*, *G. uliginosa* and hybrids : relation between terminal pedicel and height of plant.

pure *G. amarella* were both present within 50 yards of this population. At Whiteford Burrows no pure *G. uliginosa* could be found, although one or two plants in the population (520) were very nearly typical *G. uliginosa*. Phenotypically, this population consisted of about half apparent hybrids and half apparent *G. amarella*. Lousley (1950, as Llanmadog) recorded that in this locality there were at least 30 plants of *G. uliginosa*, sometimes even mixed with *G. amarella* which was abundant. He stated that the plants remained distinct and easily separable, apparently having noted no sign of hybridisation.

It seems certain that where they grow together the two species hybridise fairly readily. There appears to be a tendency for *G. uliginosa* to be more or less swamped by *G. amarella*



U4 : *G. uliginosa* : Oxwich, Glamorgan. 319/6 : *G. uliginosa* : Usedom, Pomerania.
U70 : *G. amarella* × *uliginosa* : Whiteford Burrows, Glamorgan.

although at the stage reached at Oxwich and Whiteford there are still very obvious signs of *G. uliginosa* in the population. So far as Table 7 can be accepted, the pollen fertility in the hybrids, while low, is not particularly so. Coupled with the observation that all stages of intermediacy occur (i.e. the hybrids represent not only F_1 s but also probably F_2 s and backcrosses) it must be concluded that introgression occurs between the two species. It would, of course, be necessary to carry out breeding experiments to confirm this.

The distribution of Race II of *G. amarella*, the Bristol Channel Race, is similar to that of *G. uliginosa* with the addition of the dunes of N. Devon. Some of its characteristic features, such as the longer terminal pedicel, the unequal and relatively longer calyx-teeth, and the broader leaves are reminiscent of *G. uliginosa*, and it seems possible that its unusual features may be owing to past introgression from that species.

The Continental *G. uliginosa* has some similarity with the hybrids, but until more material can be seen (preferably in the field) it would be unwise to assume hybridisation on the Continent. It seems at least possible that some of the discrepancies observed in British populations of *G. uliginosa* (e.g. those between 438 and 518/519) might be accounted for by hybridisation with *G. amarella*. If this is so, since the three populations are apparently "good" *G. uliginosa*, this presumably takes the form of slight introgression from *G. amarella* at some time in the past, the results of which appear sporadically.

TAXONOMY AND DISTRIBUTION

Gentianella uliginosa (Willd.) Börner (1912). (Plate 14).

Gentiana uliginosa Willd. (1797)

Annual or biennial. Plant 1-5 cm. high, of 0-2 (- 3) internodes. Terminal internode and terminal pedicel very markedly elongated, together usually forming from $\frac{1}{2}$ to $\frac{7}{8}$ of the height of the plant. In the larger (biennial) plants usually with long flowering branches from the base, which give the whole plant a characteristically pyramidal habit. The smaller annual plants usually consist of no more than a basal rosette of 4-8 leaves with 1 or 2 flowers arising directly from the rosette. Stem often winged in large plants. Basal leaves lanceolate (annuals) to obovate or spatulate (biennials). Stem leaves ovate or ovate-lanceolate, acute or subacute, more or less widened at the base. Flowers pentamerous or tetramerous. Calyx-teeth more or less spreading, usually equalling or exceeding the corolla, very unequal. Corolla 1.0 (annuals) - 2.0 (- 2.3) cm. long, bluish purple. Flowering (July -) August-November.

This description refers to the British plants of *G. uliginosa*. These differ in a number of respects from those Continental plants I have seen. However, Willdenow's original description refers to the height of the plants as one or two inches, and describes them as branched. These remarks agree better with the British plants than with those Continental plants examined. In these, the plants are often larger, with up to 6 internodes, and are not usually branched. The calyx-teeth are less unequal, and not usually quite as long as the corolla.

The differences between this species and *G. amarella* are constant and well-marked. The species occurs within the range of *G. amarella*, and forms hybrids with that species. Apart from these hybrids there is no confusion, and the species is retained. The agreement with Continental material from north Germany is close. I have seen photographs of *G. uliginosa* from Willdenow's herbarium in Berlin; the specimens are very similar to the Welsh plants. The peculiar distribution of the British plant (dune-slacks of South Wales) is difficult to explain. In Europe the plant grows in damp pastures and there is a

break of about 600 miles between its habitats there and the British ones, although suitable habitats apparently occur on the coasts of Norfolk and Lincolnshire.

Some slight difficulty arises over Murbeck's use of the name *G. uliginosa*. Of the *exsiccata* cited by Murbeck (1892) the following have been examined: Billot, *Fl. Gall. et Germ.*, no. 821; F. Schultz, *Herb. Norm. Cent.* 3, no. 319.

Both these, and the specimen figured in Wettstein (1896), agree well with British *G. uliginosa* (but possibly even better, in some cases, with *G. amarella* × *uliginosa*). Both Wettstein and Murbeck give the range of *G. uliginosa* as extending to Sweden. Specimens which were seen and confirmed by Murbeck as *G. uliginosa* from Sweden are in Herb. Univ. Oxon. (Dörfler, *Herb. Norm.* nos. 3773 and 3774). These are very like *G. amarella* subsp. *amarella* and do not even appear to be annuals. They have no resemblance to *G. uliginosa* in its north German form. As Lousley (1950) pointed out, the Scandinavian workers have a very different idea of *G. uliginosa* from the British authors, and from Willdenow also.

Distribution: Damp dune slacks in South Wales, v.cs. 41, 44, 45.

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NOTES ON ANNUAL SPECIES OF *SALICORNIA* IN BRITAIN

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The genus *Salicornia* is a notoriously difficult one, unless all the annual plants are regarded as belonging to one very variable species, as is sometimes done, particularly by those who have little acquaintance with them in the field. During the past century various workers in this country and the adjacent parts of the continent have recognised and attempted to define a number of taxa, mainly as a result of field observation and the examination of living material.

Among the pioneer work may be mentioned Woods' (1851) on species from the south coast of England, Dumortier's "Bouquet du littoral Belge" (1868), and Duval-Jouve's classic account of the southern French species (1868). In the early years of this century, Moss initiated a fresh attack on the problems presented by the annual species of *Salicornia* found on the English coast and on the neighbouring French coast. The results of this work were published in 1911 and 1912, and, in collaboration with Salisbury, in 1914. Shortly after the war of 1914-18, when Moss had gone to South Africa, Wilmott began an extensive study of the genus as represented in Britain. In this he had the assistance of N. D. Simpson and Miss M. S. Campbell at various times. A great amount of herbarium material, drawings, photographs and notes were accumulated (now in Herb. Mus. Brit. and Herb. N. D. Simpson), but unfortunately Wilmott died before he had produced an account of the genus in a form suitable for publication. Through the kindness of Dr. G. Taylor and Mr. J. E. Dandy we have had access to the material in the British Museum (Natural History) and we have derived valuable information from it. We had hoped to be able to make available a portion of the great amount of work and knowledge contained in these notes but this has, for various reasons, proved impossible.

The following notes are the product of field work during the past six years, combined with cultivation and cytological investigation. An attempt has been made to assess the value of the various characters which have been used to delimit species and to determine the correct application of the various names in current use in Britain. We find ourselves in agreement with the conclusion reached by the late A. J. Wilmott that a number of undescribed species exist in this country. Four of these are now sufficiently well-known to us to make descriptions possible, but there are undoubtedly others in Britain and elsewhere in Europe which still require investigation.

GENERAL MORPHOLOGY

The *Salicornia* plant has a normal root system, usually of considerable extent, but the aerial parts of the plant are highly 'reduced.' The leaves are opposite, decussate and fleshy, and consist of a small free portion extending upwards from the node, and a larger portion extending downwards over the whole of the internode below. The greater part of each leaf is 'fused' to the corresponding part of the other member of the pair, thus forming a green succulent false cortex to the stem (the 'sterile segment'). The main part of the well-branched vascular supply of the leaf runs downwards through this 'cortex.' The inflorescence consists of 3-flowered cymes (rarely solitary flowers), each

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subtended by a leaf, and occupies the distal parts of the main stem (the 'terminal spike') and branches. The flowers have a fleshy, 3-lobed perianth, more or less immersed in the succulent bracts, one or two stamens, and a solitary ovary with two freely branched stigmas.

In the older parts of the stems the leaves decay and only the woody true stem, which has some secondary thickening of the usual chenopodiaceous type, remains. As a result of this construction the whole plant has a jointed appearance, the internodes in the inflorescence ('fertile segments') being considerably shorter than those in the rest of the plant.

ASSESSMENT OF TAXONOMIC CHARACTERS

(a). *Habit*. Habit formed the basis of practically all previous classifications of the genus, but, though prostrate phenotypes of certain species are not infrequent, genotypically prostrate plants appear to be uncommon. Seed from a considerable number of prostrate plants has been grown in cultivation and only one collection, of *S. pusilla* (from Gibraltar Point, S. Lincs.), gave prostrate progeny. Plants of most species are liable to fall over at various stages in their growth, owing to waves, tidal currents and other accidents; these often continue to grow and are sometimes not easy to distinguish from plants which have grown more or less horizontally in the first place. It therefore seems unwise, at least at present, to regard habit as having any classificatory value.

(b). *Branching*. Both the degree and angle of branching appear to be useful taxonomic characters, provided that they are used with caution and that allowance is made for the considerable amount of phenotypic variation which occurs. All species, even the potentially most richly branched, can, under the influence of competition, become nearly or quite unbranched. Under favourable conditions certain species regularly show abundant tertiary branches, while others are normally less branched. The offspring of depauperate plants when cultivated in favourable conditions developed the normal branching of the species to which they belonged.

The length of the lower branches in relation to the main stem also provides a useful character if 'normal' well-grown plants are considered.

The degree of branching and length of branches are always increased by injury to the terminal spike and often also by the plant falling over or being phenotypically prostrate.

Two other branching characters were used by Moss: the occurrence of more than two branches at a node and the branching of the flower spikes. Our observations indicate that these characters occur sporadically in a considerable number of species and, though probably genetically controlled, do not appear to be closely correlated with any other characters. It does not, therefore, seem possible to use them for delimiting taxa.

(c). *Inflorescence*. (i) Morphology of the spikes. Moss and other authors have used the length, shape and number of fertile segments in the terminal spike as taxonomic characters. These all appear to provide valuable criteria, provided that well-grown 'normal' plants are examined but, as with branching and other characters, there is considerable phenotypic variation.

(ii) Morphology of the fertile segments. Little or no reference to this is to be found in the literature, though Wilmott had developed an elaborate system for its accurate description; this is unfortunately too complex for ordinary use.

There appears, once again, to be some phenotypic variation in the fertile segments but on the whole they provide useful characters. These have, however, the drawback that they are difficult to describe in a readily understandable way, are lost on drying, and often somewhat distorted by preservative fluids. The most useful features are the outline of the

segment and the width of the scarious border at its top. The shapes of segment can be roughly grouped into 10 arbitrary classes, shown in Fig. 1, but intergrading occurs between several of these.

The apparent separation of the lateral flowers by the central one was used by Moss in defining *S. dolichostachya* but it is a character common to most tetraploid species and is not constant even within a single population.

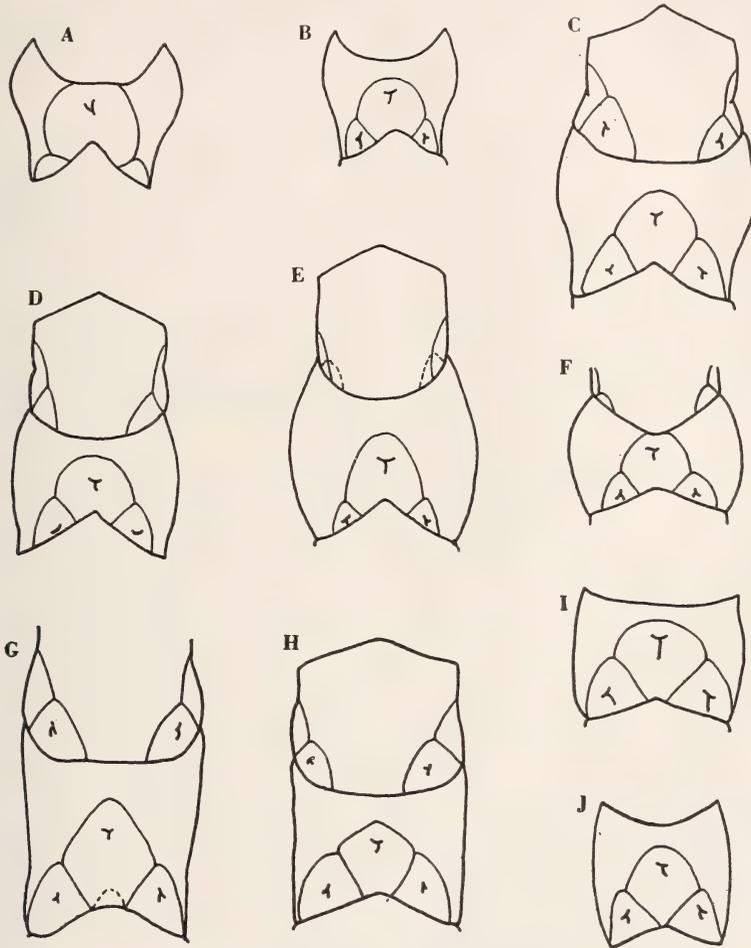


Fig. 1. Types of fertile segments.

(d). *Colour and surface texture.* These appear to be of considerable taxonomic significance, if allowance is made for the variation which is apparently correlated with edaphic factors. Species which normally colour brightly remain dull green when growing on ill-drained muds, but colour earlier than usual on relatively dry or sandy substrata. Species which normally have a matt surface often become polished on sandy soils, presumably owing to the mechanical destruction of the small globular hairs by the sand grains. **The way** in which the colour appears, whether diffuse or localized round the flowers or the upper margins of the segments, is also a valuable character.

(e). *Microscopic characters.* De Fraine (1912) suggested that the occurrence and distribution of spiral cells and 'steroids' were of taxonomic significance and her data were used by Moss. More recently Miss M. S. Campbell (unpublished) has thrown doubt on the

value of this character, a doubt which appears from our preliminary investigations to be well founded. A thorough examination of the occurrence, development and connection between these peculiar types of cells, and their possible correlation with factors such as substratum, drainage and amount of submergence, would be very desirable.

Two chromosome numbers, $2n = 18$ and 36 , are found among the annual species of *Salicornia* in Britain, and many characters, both macroscopic and microscopic, show a correlation with chromosome number. These correlations, which are set out in Table 1, appear to be sufficiently good for chromosome number to be predicted from morphology.

TABLE 1.

Character	$2n$	$4n$
Angle of branching of the uppermost branches	c. 45° , \pm straight	$45-90^\circ$, curving upwards.
Fertile segments :		
No. in terminal spike	1-12 (- 22)	(6 -) 10-25 (- 32)
Types (Fig. 1)	A-F	G-J
max. width/width at base	1.1-1.4	1.0-1.2
Central flower of cyme	usually larger than visible part of lateral flowers	about equalling visible part of lateral flowers
Free part of leaf	1 mm. or more, acute	rarely more than 1 mm., obtuse to subacute
Stamens	0-1 (- 2), exerted or not	(1 -) 2, always exerted.
Anthers	0.4-0.6 mm.	0.65-0.9 mm.
Pollen grain diam.	(20 -) 24-28 (- 31) μ	(27 -) 31-34 (- 42) μ
Length of stomata on sterile segments at base of terminal spike	(20 -) 24-30 (- 33) μ	(27 -) 29-36 (- 42) μ
Length of seeds	1.0-1.7 mm.	(1.3 -) 1.5-2.3 mm.

THE COLLECTION OF ANNUAL SALICORNIA SPECIES

For identification it is desirable to collect a number (preferably 10-12) of well-grown specimens from each population, rejecting any which have fallen over or which have damaged main stems. Damage due to boring larvae is often inconspicuous but may profoundly alter the habit of the plant, the length of the spikes and the shape of the segments. The identity of small poorly-branched plants growing in dense stands is best judged by comparison with well-grown plants in the vicinity.

Identification is usually easiest when the plants are mature and the characteristic colours have developed; this is generally in September or October, according to species and locality. Fresh material is very much easier to identify than even the best preserved plants.

ECOLOGY

Salicornia species may occur in the whole range of salt-marsh habitats and even on sheltered beaches of muddy shingle, while *S. pusilla* and *S. ramosissima* are sometimes found on the landward side of sea-walls.

The chief types of habitat and the species most commonly found in them are :

- (1) The drift line : *S. pusilla*, *S. ramosissima*.

- (2) The upper parts of the marshes, often just below a sea wall : *S. ramosissima*, *S. obscura*, *S. lutescens*, *S. pusilla*.
- (3) 'General' salt marsh :
 - (a) in more or less closed communities : *S. ramosissima*, *S. obscura* (rather rare)
 - (b) in salt-pans : *S. obscura*, *S. nitens*, *S. ramosissima*.
- (4) Sides of channels : *S. fragilis*, *S. obscura*, *S. ramosissima*.
- (5) Open or sandy mud at low levels : *S. dolichostachya*, *S. europaea*, *S. lutescens*, *S. fragilis*.
- (6) Firm muddy shingle : *S. ramosissima* (prostrate forms).

KEY.

-
- 1. Cymes regularly 1-flowered; terminal spikes up to c.6 mm. **4. pusilla**
 - 1. Cymes normally 3-flowered; terminal spikes usually more than 6 mm.
 - 2. Fertile segments of types A-F (Fig. 1); stamens 1, very rarely 2 in a few flowers; anthers 0.4-0.6 mm.; seeds 1.0-1.7 mm.
 - 3. Plant dark shining green, often becoming dark purplish-red; fertile segments of types A and B (Fig. 1) with a conspicuous scarious border c. 0.2 mm. wide at top. **1. ramosissima**
 - 3. Fertile segments of types C-F (Fig. 1) with a narrow scarious border not more than 0.1 mm. wide.
 - 4. Plant clear green, becoming yellow and red or pinkish; lower primary branches up to as long as main stem; tertiary branches usually present; fertile segments of types E and F (Fig. 1). **2. europaea**
 - 4. Plant dull glaucous green, fertile spikes dull yellow, rarely purplish round the flowers; lower primary branches usually less than $\frac{1}{2}$ as long as main stem, tertiary branches 0; fertile segments of types C and D (Fig. 1). **3. obscura**
 - 2. Fertile segments of types G-J (Fig. 1); stamens usually 2; anthers 0.7-0.9 mm.; seeds (1.3 -) 1.5-2.3mm.
 - 5. Terminal spike cylindrical, very obtuse; fertile segments up to 12 (-15); plant clear green becoming bright yellow or purplish.
 - 6. Plant becoming clear brownish-purple to brownish-orange; fertile segments rarely exceeding 3 mm. long. **5. nitens**
 - 6. Plant becoming bright yellow or yellow-green, rarely with diffuse pink colour; fertile segments usually more than 3 mm. long (if plant is dull green see *S. fragilis*). **8. lutescens**
 - 5. Terminal spike distinctly tapering, acute or \pm obtuse; fertile segments 12 or more; plant dull yellow (sometimes pinkish on sandy mud).
 - 7. Lower primary branches very rarely more than $\frac{1}{2}$ as long as main stem, their spikes cylindrical. **6. fragilis**
 - 7. Lower primary branches usually more than $\frac{1}{2}$ as long as main stem, their spikes distinctly tapering. **7. dolichostachya**
-

DESCRIPTION OF SPECIES

A. Diploid species.

- 1. *S. ramosissima* Woods (1851). *Bot. Gaz.* **3**, 29.

Erect or prostrate, up to 40 cm. high; typically freely branched and bushy, but very variable and often forming pure stands of simple or slightly branched plants in salt-pans; lowest branches usually shorter than main stem, very rarely with more than 2 branches at a node. Plant dark green; sterile segments becoming yellow-green then dark purplish; fertile segments soon becoming dark purple round the flowers and upper margin, the remainder either remaining dark green or becoming purple or, rarely, yellowish. Terminal spike (5 -) 10-30 (-40) mm., \pm tapering, with (1 -) 4-9 (-12) fertile segments of types A and B (Fig. 1). Fertile segments (2nd-4th from base of terminal spike) 1.9-3.5 mm. long, 2.0-4.0 mm. diam. at base and top and 2.7-5.3 mm. diam. just above the middle. Free

part of leaf (0.7 -) 1 mm. or more, acute, with a conspicuous scarious border c. 0.2 mm. wide. Central flower 1.5-2.3 × 1.4-2.7 mm., rounded-rhomboid to almost circular, the upper edge not more than 0.5 mm. from top of segment. Lateral flowers 1.3-2.1 × 1.0-2.1 mm., the visible part much smaller than the central flower. Flowers August-September. $2n = 18$. In all parts of salt-marshes except the lower mud-flats. Widespread and common in E. and S. England and S. Wales. Distribution elsewhere uncertain. Plants from S. and E. Ireland differ in being clear green, becoming yellow tinged with pink to crimson, and in the terminal spike being cylindrical and obtuse. These differences appear to be maintained in cultivation, but further investigation is required.

S. gracillima (Townsend) Moss was described as a small plant with very short primary branches, short terminal spike and 'steroids' in the fertile segments. Offspring of similar plants from the type locality (Pagham Harbour, W. Sussex) were large and much-branched and apparently identical with *S. ramosissima*. *S. prostrata* auct. angl. (incl. Moss, Butcher, and Tutin) is described as prostrate with long widely spreading lower branches. The progeny of plants of this kind have so far proved to be erect in cultivation and to resemble *S. ramosissima*, except that the angle of the lower branches is often c. 90° (instead of c. 45°), the plant colours more rapidly, and the spikes are rather more slender. Many intermediates occur. *S. appressa* Dumort. and *S. smithiana* Moss are doubtfully distinct from *S. prostrata* auct. and appear to behave in the same way in cultivation. *S. prostrata* Pallas, with which British plants have been regarded as conspecific, was described from the N.W. coast of the Caspian. The description is uninformative and the figure is that of a plant, probably diploid, in flower. It is at present impossible to be certain of the identity of Pallas's plant but, as was pointed out by Townsend (1904), it is in any case unlikely that it is the same as any found in western Europe.

2. *S. europaea* L. (1753). *Sp. Pl.*, 3.

S. herbacea L. (1762) *Sp. Pl.*, ed. 2, 5, ? *S. stricta* Dumort. (1868) *Bull. Soc. Bot. Belg.*, 7, 334.

Erect, (10 -) 15-30 (- 35) cm. high; typically freely branched; lowest branches up to as long as the main stem; rarely with more than 2 branches at a node. Plant dark green; sterile segments becoming yellow-green to yellow, then pink or red before collapsing; fertile segments soon becoming yellowish, then rather diffuse pink or red starting round the flowers. Terminal spike (10 -) 15-50 mm., slightly tapering, obtuse, with (3 -) 5-9 (- 12) fertile segments of types E and F (Fig. 1). Fertile segments (3rd and 4th from base of terminal spike) 2.5-4 mm. long, 3.0-4.5 mm. diam. at base and top and 3.5-6 mm. diam. at about the middle. Free part of leaf c. 1 mm., acute, with an inconspicuous scarious border c. 0.1 mm. wide. Central flower 1.7-2.5 × 1.7-2.5 mm., rounded above, the upper edge not more than 0.5 mm. from top of segment. Lateral flowers 1.6-2.0 × 1.3-1.8 mm., the visible part much smaller than the central flower. Flowers August. $2n = 18$. Open sandy mud, rather local. S. and W. coasts of England. ? Ireland. W. Europe. The only diploid species occurring at low tidal levels. Irish plants appear to differ only in the longer terminal spikes with 10-22 fertile segments.

Dumortier's description of *S. stricta*, "Herbacea, caule ramisque erectis, fastigiatis", would apply to the majority of W. European species. In 1935 Mr. N. D. Simpson examined the type (in Herb. Jard. Bot. Bruxelles) and visited the probable type locality (Nieupoort). The specimens collected by him, as being almost identical with the type, appear to be similar to *S. europaea*. However, it should be pointed out that, with dried specimens, only the characters of habit and branching can be observed, and that under these circumstances it is very doubtful whether *S. europaea* (or any other diploid, 3-flowered species)

can be distinguished from the very variable *S. ramosissima*, which according to Simpson also occurs in Nieuport.

S. stricta auct. angl. (including Townsend, Moss, Butcher & Strudwick, and Hambler) appears to be a composite species made up of *S. obscura*, *S. fragilis* and *S. lutescens*.

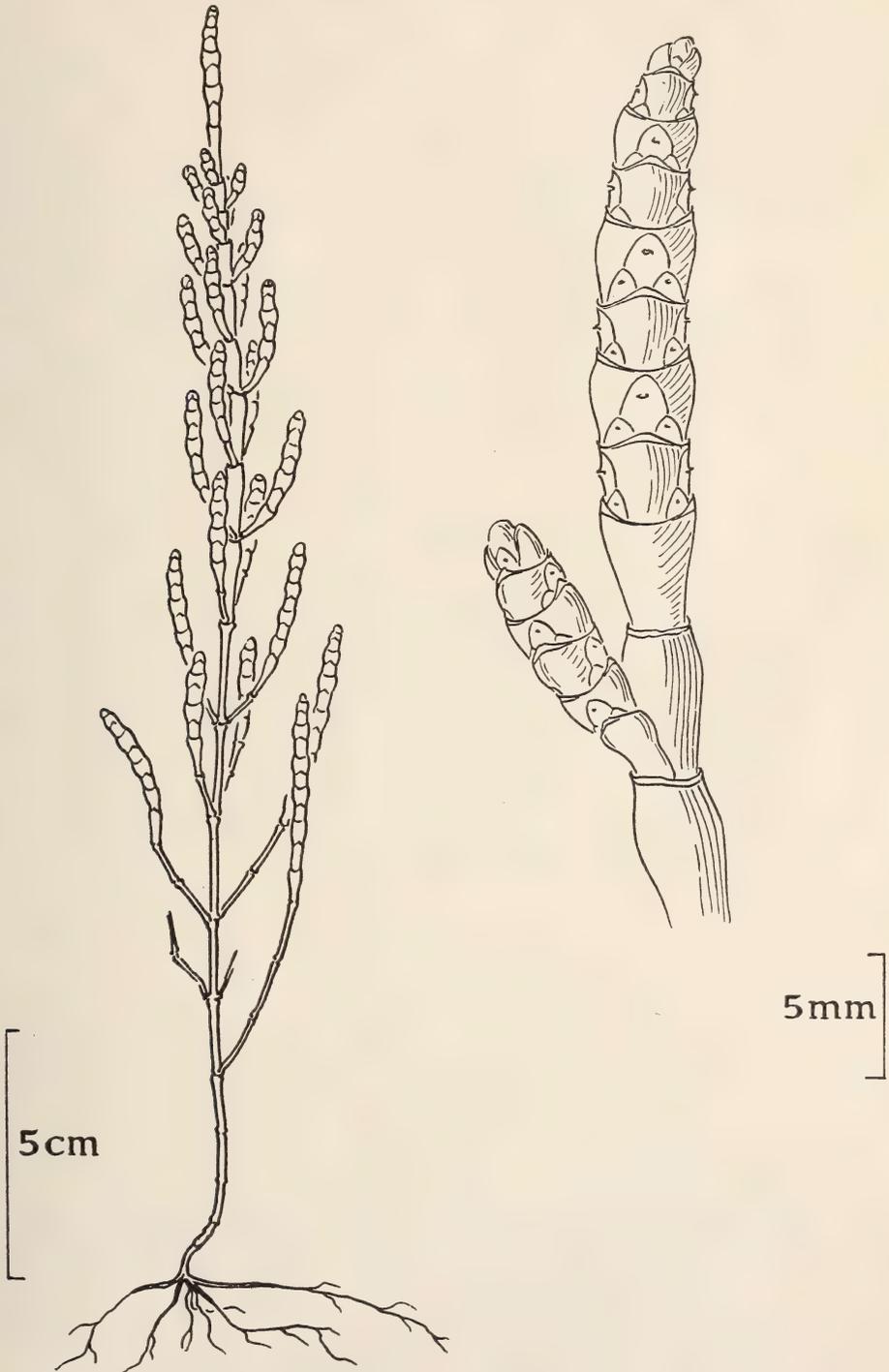


Fig. 2. *Salicornia obscura*.

3. *S. obscura* P. W. Ball & Tutin (Fig. 2).

Erect, 10-40 (- 45) cm. high, commonly with primary branches only; lowest branches not more than half as long as main stem, usually less. Plant dull, slightly glaucous, green, usually with matt surface; sterile segments becoming dull yellow just before collapsing. Fertile segments becoming dull yellowish-green, rarely with a slight purple colour round the pores of the flowers. Terminal spikes 10-40 (- 45) mm. long, nearly cylindrical, obtuse, with (3 -) 5-9 (- 14) fertile segments of types C and D (Fig. 1). Fertile segments (2nd to 4th from base of terminal spike) 2.5-4.5 mm. long, 2.8-4.0 (- 5.0) mm. diam. at base and top with a maximum diameter of 3.2-5.0 (- 5.5) mm. usually above the middle. Free part of leaf c. 1 mm. long, triangular, acute, with a very narrow scarios border. Central flower 1.35-3.1 × 1.5-2.5 mm., semicircular above, the upper edge not more than 0.7 mm. from the top of the segment. Lateral flowers 1.5-2.7 × 1.5-2.7 mm., the visible part small, more or less triangular. Stamens usually solitary and not exerted. Seeds 1.1-1.7 mm. Flowers August-September. $2n = 18$. On bare damp mud, in salt-pans and at sides of channels. East and south coasts from S. Lincs. to S. Hants.

Generally recognisable by the dull colour, the short, simple branches and the bulging fertile segments with narrow scarios margins and usually cleistogamous flowers. It is often difficult to separate with certainty from forms of *S. fragilis* and *S. lutescens*, except when it is in flower.

4. *S. pusilla* Woods (1851) *Bot. Gaz.* 3, 30.

S. disarticulata Moss (1911)

Erect or prostrate, up to 25 cm., usually much branched and bushy. Plant yellowish-green, becoming brownish- or pinkish-yellow. Terminal spike up to c. 6 mm., with 2-4 fertile segments. Cymes 1-flowered. Flowers almost circular, often brownish. Fertile segments eventually disarticulating. Flowers August-September. $2n = 18$. In the drier parts of salt-marshes and particularly along the drift line. Dorset to Kent, Essex, Norfolk; Carmarthen; Waterford. N.W. France.

A very distinct species, readily recognised by its solitary flowers and disarticulating fertile segments. The identity of *S. pusilla* sensu Moss, described as a small, little-branched species with 3-flowered cymes, remains quite obscure.

B. Tetraploid species.

5. *S. nitens* P. W. Ball & Tutin (Fig. 3)

Erect, 5-25 cm. high, usually with primary branches only; lower branches usually less than $\frac{1}{4}$ the length of the main stem, upper branches generally curving upwards at the tip. Plant green to yellowish-green with a smooth, shining, somewhat translucent appearance; sterile segments widened conspicuously near the top, soon becoming clear light brownish-purple to brownish-orange. Fertile segments soon becoming light brownish-purple, the colour appearing more or less diffusely, but at first particularly in the flowers and just below the upper edge of the segment. Terminal spike 12-40 mm. long, cylindrical, obtuse, with 4-9 fertile segments of type J (Fig. 1). Fertile segments (2nd to 4th from the base of the terminal spike) (1.8 -) 2.0-3.0 (- 3.5) mm. long, 2.0-4.0 mm. diam. at base and top and a maximum diameter of 2.3-4.5 mm. about the middle. Free part of leaf c. 0.5 mm. long, subobtuse, with narrow scarios border. Central flowers 1.1-2.2 × 1.1-1.8 mm., semicircular above. Lateral flowers 1.2-1.8 × 1.0-1.7 mm., the visible part triangular, almost as long as the central flower. Seeds 1.5-1.7 mm. Flowers

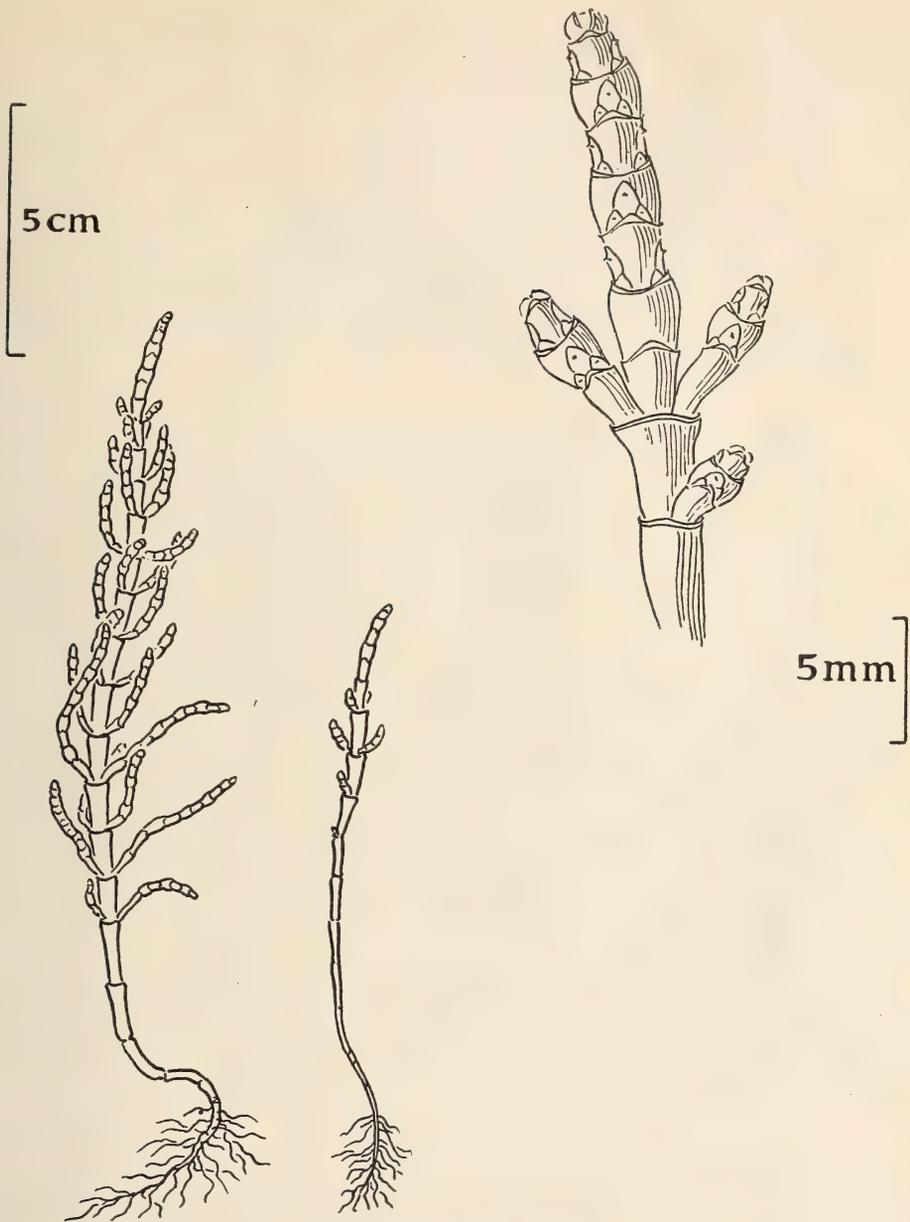


Fig. 3. *Salicornia nitens*.

September. Probably tetraploid. Bare mud and in pans in the upper parts of salt-marshes. S. and E. England, apparently common in suitable habitats from E. Suffolk to Hants. Distribution elsewhere unknown.

6. *S. fragilis* P. W. Ball & Tutin

Erect, (10 -) 15-35 (- 40) cm. high, usually with primary branches only; lowest branches usually less than $\frac{1}{4}$ the length of the main stem; rarely more than 2 branches at

a node. Plant dull, often slightly glaucous green; sterile segments becoming dull yellowish-green when mature. Terminal spike (20 -) 30-80 (- 100) mm. long, somewhat tapering, with (6 -) 8-16 (- 20) fertile segments of types G-I (Fig. 1). Fertile segments (3rd and 4th from base of terminal spike) 3.0-5.0 × 3.0-4.5 mm., more or less cylindrical. Free part of leaf not more than 1 mm. long, subobtuse, with a very narrow scarious border. Central flower 2.0-3.0 × 1.8-3.0 mm., semicircular to triangular above, the upper edge at least 0.5 mm. from the top of the segment. Lateral flowers 2.0-2.5 × 1.8-2.2 mm., the visible part more or less triangular and almost as long as the central flower. Seeds 1.5-2.0 mm. Flowers August-September. $2n = 36$. Bare mud at sides of channels and in the lower levels of salt-marshes. E. Suffolk to Kent. Distribution elsewhere unknown.

S. fragilis shows an inverse correlation between the length of the terminal spike and the abundances of branches.

7. *S. dolichostachya* Moss (1912) *New Phytol.* **11**, 409.

Erect 10-40 (- 45) cm. high, abundantly branched and bushy; lower primary branches usually about as long as main stem; often more than 2 branches at a node. Plant dark green; sterile segments becoming paler or dull yellow then brownish before collapsing. Fertile segments usually becoming paler, rarely dull yellow or with a slight diffuse purple tinge. Terminal spike (25 -) 50-120 (- 200) mm., distinctly tapering but often obtuse, with (7 -) 12-25 (- 32) fertile segments of types G-I (Fig. 1). Lateral spikes tapering, subacute, those of the longest primary branches often nearly as large as the terminal spike. Fertile segments (3rd and 4th from the base of the terminal spike) 3.0-6.0 × 3.0-6.0 mm., nearly cylindrical. Free part of leaf c. 1 mm. or less, subobtuse, with a very narrow scarious border. Central flower 2.4-4.0 × 1.9-2.9 mm., triangular to semicircular above, the upper edge at least 0.5 mm. from the top of the segment. Lateral flowers 1.8-3.0 × 1.5-2.3 mm., the visible part triangular and almost as long as the central flower. Flower July-August. $2n = 36$. On open mud or sandy mud in the lowest zone of salt-marshes, occasionally on the sides of narrow channels in the middle zone. Coasts of Great Britain from Lancs. to Devon, Kent and E. Ross; S. and E. coasts of Ireland, W. Galway, Netherlands, Denmark.

S. dolichostachya is the chief coloniser of open mud and muddy sand in many places. It is abundant on gradually sloping intertidal flats which are not too exposed, and it appears to require frequent submersion. The habit varies from straggling to strongly fastigiate. The taxon, as delimited here, possibly includes more than one species.

8. *S. lutescens* P. W. Ball & Tutin (Fig. 4).

Erect, (10 -) 15-30 (- 40) cm. high, usually abundantly branched and bushy; lowest branches up to 2/3 (- 1) the length of the main stem; very rarely more than 2 branches at a node. Plant green to yellowish-green; sterile segments soon becoming yellow, occasionally with a diffuse purplish tinge. Terminal spike (15 -) 25-60 (- 70) mm., cylindrical, obtuse, with (5 -) 8-12 (- 16) fertile segments of types G-I (Fig. 1). Fertile segments (3rd and 4th from base of terminal spike) 3.3-5.0 × 3.5-6.0 mm., more or less cylindrical. Free part of leaf not more than 1 mm., subobtuse, with a very narrow scarious border. Central flower 2.0-3.5 × 2.0-2.5 mm., semicircular to triangular above, the upper edge at least 0.5 mm. from the top of the segment. Lateral flowers 1.8-2.5 × 1.7-2.5 mm., the visible part triangular, almost as long as the central flower. Seeds 1.4-2.1 mm. Flowers July-August. $2n = 36$. Usually on firm and comparatively dry mud or muddy sand. Coasts of England from S. Lincs. to S. Hants.; Glamorgan, Merioneth.

Distribution elsewhere unknown.

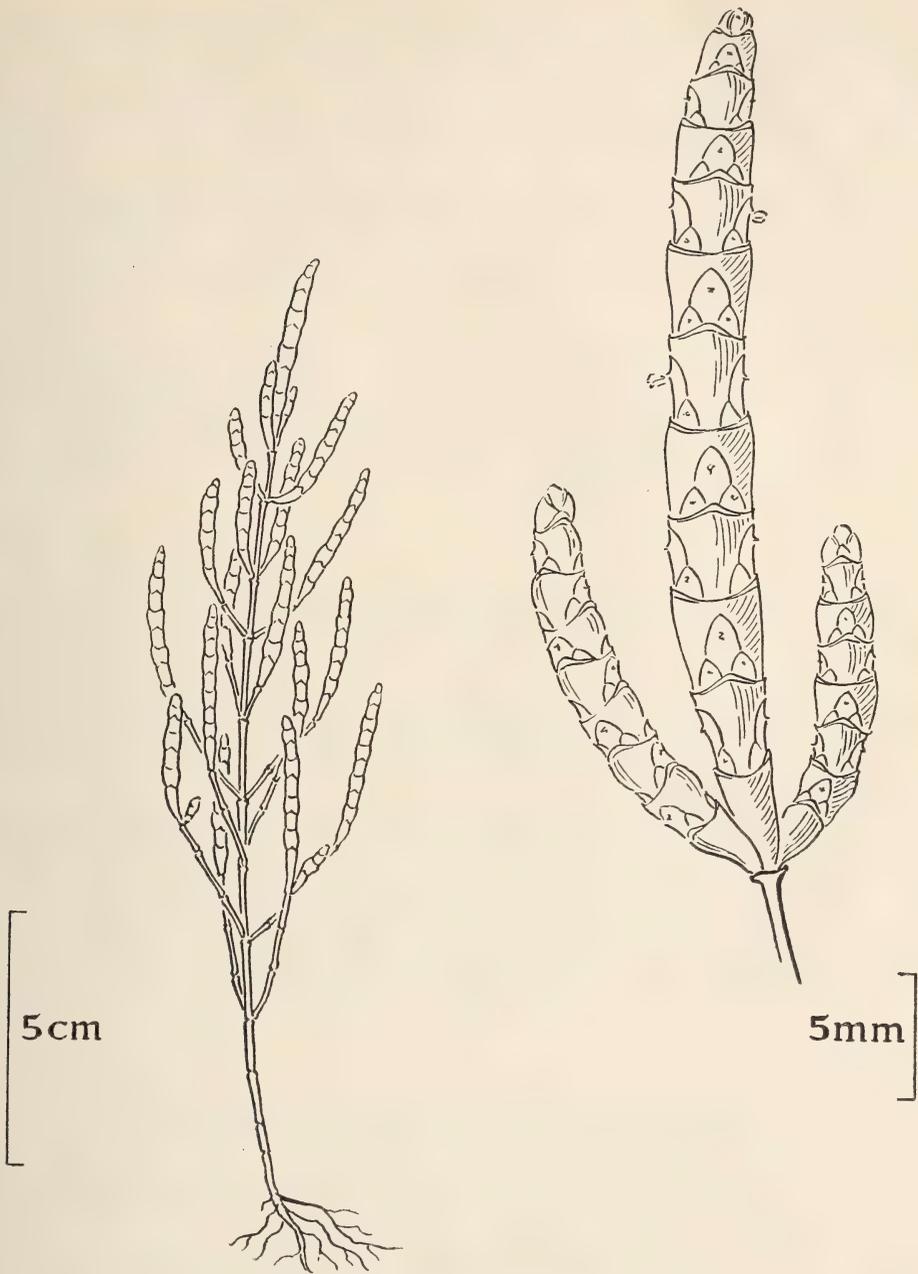


Fig 4. *Salicornia lutescens*.

Diagnoses of new species.

S. lutescens sp. nov. *S. dolichostachyam* similans, sed colore laete viridi vel flavo-viridi mox laete lutescente, spicis terminalibus brevioribus (25-60 mm.) cylindricis obtusis cum segmentis fertilibus paucioribus (8-12) praeditis differt. Typus in Herb. Mus. Brit. : North bank of R. Ogmore, Glamorgan (v.c. 41). Upper part of sandy salt-marsh. Leg. A. Loosemore & B. Miles. September, 1957.

S. fragilis sp. nov. A *S. dolichostachya* ramis lateralibus brevibus ipsis raro iterum ramosis, spicis terminalibus brevioribus (30-80 mm.) cum segmentis fertilibus paucioribus (8-16) praeditis diagnoscutur; praeterea a *S. lutescente* habitu ramoso, colore haud laete lutescente, spicis terminalibus ad apicem attenuatis differt. Typus in Herb. Mus. Brit. : Leigh-on-Sea, South Essex (v.c. 18). Mud flats on side of a broad channel. Leg. P. W. Ball. September 1956.

S. obscura sp. nov. A *S. europaea* ramis primariis plerumque brevibus ipsis raro iterum ramosis, colore opaco subglauescenti-viridi demum hebeti-flavescente, superficie opaca haud nitente, habitu fere semper cleistogamo differt. Typus in Herb. Mus. Brit. : North Hayling, S. Hampshire (v.c. 11). Pan in upper part of salt-marsh. Leg. P. W. Ball. September, 1957.

S. nitens sp. nov. A *S. obscura* superficie levi nitente subtranslucente, colore laete viridi vel flavo-viridi mox pallide brunneo-purpureo vel gradatim brunneo-aurantiaco, segmentis sterilibus sub apicem conspicue inflatis, habitu chasmogamo differt. Typus in Herb. Mus. Brit. : North Hayling, South Hampshire (v.c. 11). Bare mud in upper part of salt-marsh. Leg. P. W. Ball. September, 1957.

SUMMARY.

An attempt is made to assess the value of the characters used in defining species of *Salicornia*, taking into account evidence from culture experiments as well as field observation.

Notes are given on the collection, preservation and habitat preferences of the annual species of *Salicornia*, together with a key for their identification. Diploid and tetraploid series of species are described and the correlation between chromosome number and morphological characters indicated.

The annual species of *Salicornia* recognised in the British Isles are reviewed and four new ones described. It is suggested that the name *S. prostrata* Pallas, even if it could be satisfactorily typified, is inapplicable to British plants and that plants so called, together with those known as *S. appressa* and *S. smithiana*, are phenotypes of *S. ramosissima*. The identity of '*S. gracillima*' is discussed and it is concluded that on present evidence this taxon cannot be maintained as a species distinct from *S. ramosissima*.

ACKNOWLEDGEMENTS

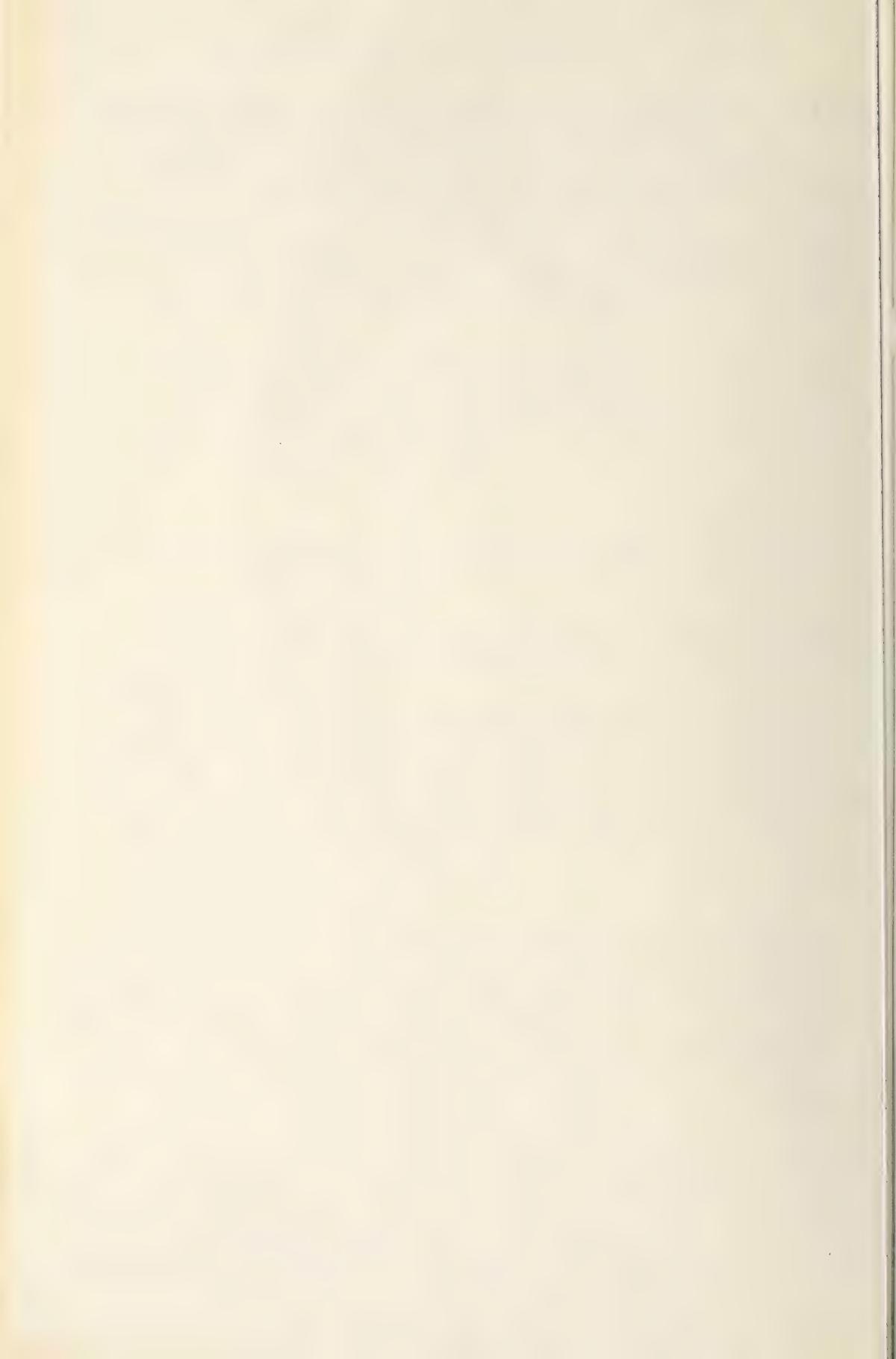
We are greatly indebted to the following for assistance in many different ways : Miss M. S. Campbell, Dr. D. H. Dalby, Mr. J. E. Dandy, Miss E. J. Gibbons, Mr. N. Y. Sandwith, Mr. N. Douglas Simpson, Dr. G. Taylor and Professor D. A. Webb. The figures of *S. lutescens*, *S. nitens* and *S. obscura* were drawn by Miss S. J. Roles and are reproduced by permission of the Cambridge University Press.

Much of the work was done by one of us (P.W.B.) during the tenure of a Maintenance Allowance from D.S.I.R..

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THE IDENTITY OF *ARENARIA GOTHICA* AUCT. ANGL.

By G. HALLIDAY

Department of Botany, Leicester University.

Arenaria gothica Fr. is commonly distinguished from the complex of the perennial *A. ciliata* L. *sensu lato* on the basis of its life form. Being relatively short lived in nature, with a single or occasionally two flowering seasons, the plant is as a rule very floriferous and vegetative summer shoots are rare. So defined, it is limited in its distribution to a small area in the Swiss Jura, the Swedish island of Gotland and mainland province of Västergötland, and upper Ribblesdale in Mid-west Yorkshire, v.c. 64. This curious distribution has often aroused comment from phytogeographers who usually cite it as an extreme case of Quaternary dissection of a once continuous distribution. This is the suggested explanation put forward for example by Albertson (1946).

However, a recent comparative study of material from these three areas indicates that the taxon is not as coherent as has been supposed. The importance of critical studies of taxa used in phytogeographical arguments should be evident and has been urged most forcibly in a recent paper by A. & D. Löve (1958), concerning the amphi-atlantic plants.

The following is a preliminary account of the chief conclusions concerning *A. gothica* and the consequent taxonomic changes arising from this study. A more detailed account of the complex will be published later.

A. gothica, described from Gotland by Wahlenberg as *A. ciliata* β *multicaulis*, was raised to specific rank by Fries (1839). The plants of the Jura, referred to by Grenier and Godron (1848) as *A. ciliata* β *fugax*, were later judged by Grenier (1869) to be conspecific with *A. gothica* Fr. The Yorkshire plant was not discovered until 1889. Two varieties of the species were recognised by Rouy & Foucaud (1896), α *gothica* Rouy & Fouc. and β *jurana* (Genty) Rouy & Fouc. These were referred to respectively by Williams (1898) as α *typica* and β *fugax*, the former name being applied to the two northern populations and the latter to the more robust plants of the Jura. This distinction is seldom made in modern floras and no taxonomic distinction appears to have been made between the British and Swedish plants.

Herbarium material has been examined from all the three areas and Swedish and British plants have been studied both in the field and in cultivation. Unfortunately the latter has proved impossible for the Jura plants, which are in danger of extinction. The most important morphological differences detected in this study are presented in Table 1, together for comparison with data for the perennial species *A. norvegica* Gunn. based on material from throughout its range.

Seeds of the Jura plants proved to be significantly larger than those of the Swedish or British ones (p being less than 0.1%) though all fell within the range of *A. norvegica*.

From Table 1 it will be evident that with respect to these characters the affinities of the British *A. gothica* lie with *A. norvegica* rather than with the Swedish or Jura plants which it resembles in life form and ecology. The first three are however quite distinct in cultivation.

This conclusion, based on morphology, is supported by evidence from cytology and hybridisation. The Swedish plants have a diploid number $2n = 100$ (Horn, in A. & D. Löve, 1948; Blackburn *in litt.*; Halliday, 1958), whilst both the British plants and

TABLE 1.

Morphological Comparison of *A. gothica* and *A. norvegica*.

All measurements in mm.: those within the brackets indicate the extreme range; those outside, the normal.

	<i>A. gothica sens. lat.</i>			<i>A. norvegica</i>
	Jura	Sweden	Britain	
Height	(50) 80 – 120 (150)	60 – 100 (130)	30 – 50	30 – 60
Leaves				
Length	4 – 5.5 (7)	(3.5) 4 – 5 (6)	4.5 – 5 (6)	3 – 4.5 (6)
Breadth	(1.25) 1.5 – 2 (2.5)	(1.25) 1.5 – 2 (2.5)	1 – 1.5	1 – 1.5 (1.75)
Length/Breadth	2.7 – 2.75	2.5 – 2.7	3.6 – 4	3
Ciliation*	$\frac{1}{3}$ – $\frac{1}{2}$	$\frac{1}{2}$ –	0 – $\frac{1}{3}$ ($\frac{1}{2}$)	0 – $\frac{1}{3}$
Number of flowers				
per cyme	(1) 3 – 6 (8)	(1) 2 – 3 (5)	1 – 2 (4)	1 – 2 (3)
Outer sepals				
marginal cilia*	– $\frac{1}{2}$	– $\frac{1}{2}$	– $\frac{1}{3}$	0 ($\frac{1}{4}$)
cilia on back	rare	very common	never present	never present
Petal length	4 – 5.5	4 – 4.5†	(5) 5.25 – 5.5†	4 – 4.5
Flower diameter‡	—	7 – 9	11 – 12	9 – 10

* The extent to which the marginal cilia extend from the base towards the apex.

† Measured on living cultivated material.

‡ Measured in field and on cultivated material.

A. norvegica have $2n = 80$ (Blackburn & Morton, 1957; Halliday, 1958). At the present time, no chromosome numbers have been determined for the Jura plants or any central European *A. ciliata*. Hybridisation experiments reflect this cytological difference. No barriers to gene exchange appear to exist in cultivation between *A. norvegica* and British *A. gothica*, the F_1 , F_2 and F_1 backcrosses being as fertile as the parents, whereas in crosses involving either of these and Swedish material, meiotic irregularities occur in the F_1 and are associated with reduced seed-formation. This low fertility persists in the F_2 and in backcrosses to the parent with $2n = 80$ but is increased somewhat on backcrossing to the Swedish parent.

On this evidence, two ecospecies are involved, one including *A. norvegica* and British *A. gothica* and the other the Swedish *A. gothica*. There are therefore strong morphological and genetical grounds for removing the British taxon from *A. gothica* and according it either specific rank or treating it as a subspecies of *A. norvegica*. The former possibility is rejected, not only on cytogenetical grounds, but partly because of the practical difficulty in distinguishing young plants of *A. norvegica* from British *A. gothica*. It is accordingly proposed to give the British *A. gothica* subspecific rank.

A. norvegica was described by Gunnerus (1772) but, since he makes no reference to its perennial habit, the original description could cover the British plant. There are however in this a number of inadequate statements as for example “folia . . . enervia, ubique nuda (ne basi quidem ciliata) nitentia.” Therefore descriptions of the two subspecies together with an emended species description are given below.

ARENARIA NORVEGICA Gunn., 1772, *Flora Norvegica*, 2, 144.

An annual, biennial or perennial herb; 3–7 cm. high; leaves obovate, glabrous or ciliate to less than half way, obscurely nerved. Cymes terminal, 1–2 (–4)-flowered. Pedicels

almost glabrous, slender, 4–13 mm. Sepals ovate, 3–4 mm. long, acute with a hyaline margin, usually 3-nerved, but the lateral nerves often obscure, glabrous or with a few cilia confined to the basal margin. Petals white, 4–5.5 mm. long, exceeding the sepals. Ripe capsule equal to or slightly exceeding the calyx. Seeds black with low broad tubercles, 0.8–1.0 mm. in length. $2n = 80$.

Subsp. *NORVEGICA*

Herba perennis, caulibus densis procumbentibus, internodiis inferioribus abbreviatis, caulibus floriferis erectis. Folia semi-succulenta, viridia opaca, 3.4–5 (–6) \times 1.1–1.5 (–1.75) mm. Pedunculi terminales (4–) 5–9 (–13) mm. Sepala glabra, vel rarissime ciliis paucis ad basim marginis obsita. Petala 4–4.5 mm. Flores 9–10 mm. diametro. Styli 3–5; dentes capsularum 6–10. Semina 0.8–1.0 mm. Florens 6–9.

Norvegia, Suecia, Scotia, Islandia.

A perennial herb with dense procumbent shoots, short basal internodes, and erect flowering stems. Leaves somewhat succulent, dark green, 3.4–5 (–6) \times 1.1–1.5 (–1.75) mm. Terminal peduncles (4–) 5–9 (–13) mm. Sepals glabrous, or very rarely with a few cilia at the basal margin. Petals 4–4.5 mm. Flowers 9–10 mm. in diameter. Styles 3–5; capsule teeth 6–10. Seeds 0.8–1.0 mm. Flowering 6–9.

Norway, Sweden, Scotland, Iceland.

Subsp. *anglica* Halliday, subsp. nov. *A. gothica* α *gothica* Rouy & Fouc., 1896, *Flore de France*, **3**, 248, *pro parte*. *A. gothica* α *typica* F. N. Williams, 1898, *Journ. Linn. Soc., Bot.*, **33**, 420, *pro parte*.

Herba annua hiberna vel biennis, caulibus floriferis erectis et caulibus sterilibus aestivalibus paucis. Habitus laxior quam in subsp. *norvegica*. Folia pallide viridia, 4.5–5 (–6) \times 1.1–1.5 mm. Pedunculi terminales (4–) 6–13 mm. Sepala exteriora paucis ciliis ad basim marginis obsita vel rarissime glaberrima. Petala 5–5.5 mm. Fores 11–12 mm. diametro. Styli 3; dentes capsularum 6. Semina 0.85 mm. Florens 51–10.

Anglia.

Holotypus in Herb. Univ. Cantab.: J. F. Pickard, June 6th, 1905 "between Selside and Ingleborough, near Horton-in-Ribblesdale, Mid-west Yorks."

A winter annual or biennial herb with erect flowering stems and few sterile summer shoots. Of a laxer habit than subsp. *norvegica*. Leaves light green, 4.5–5 (–6) \times 1.1–1.5 mm. Terminal peduncles (4–) 6–13 mm. Outer sepals with a few cilia at the basal margin or very rarely entirely glabrous. Petals 5–5.5 mm. Flowers 11–12 mm. in diameter. Styles 3; capsule teeth 6. Seeds 0.85 mm. Flowering 5–10.

England.

While it seems probable that the Jura plant will prove to be equally distinct from the Swedish and more closely allied to the central European *A. ciliata*, until experimental evidence of this is obtained it seems desirable to retain it for the present in *A. gothica*. The bearing of these and unpublished results on the origin and history of the British taxa is a subject that it is hoped to raise in a later paper.

ACKNOWLEDGEMENTS

This account is based on work carried out at the Cambridge University Botany School during the tenure of a Nature Conservancy Studentship under the supervision of Dr. S. M. Walters to whom I wish to express my gratitude. I wish also to thank Dr. P. Villaret of Lausanne for the loan of herbarium material and Prof. T. G. Tutin and Dr. E. F. Warburg for suggesting improvements to the manuscript.

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JUNCUS SUBULATUS FORSK. IN THE BRITISH ISLES

By A. J. WILLIS and ELIZABETH W. DAVIES

Department of Botany, University of Bristol

In May, 1957, two colonies of a perennial rush were found in the salt marsh at Berrow on the North Somerset coast (v.c. 6), in circular patches about 10 m. in diameter that suggested vegetative spread from plants originally established perhaps some ten years before. The plant was identified as *Juncus subulatus* Forsk. after investigations had shown that it was not of hybrid origin, meiosis proving to be quite normal and the pollen good. This species occurs mainly in salt marshes along Mediterranean shores and has not been previously recorded in the British Isles. At Berrow the *Juncus* is surrounded mainly by *Scirpus maritimus*, which it has successfully displaced, but is itself sparsely interspersed with etiolated *Glaux maritima*, *Carex extensa*, *Atriplex hastata*, *Juncus gerardii*, *Triglochin maritima*, and *Aster tripolium*. The formation and the vegetational development of the Berrow salt marsh are recent and have been described by Thompson (1922, 1928, 1930), Kendall (1938), and Boley (1942).

An account is given here of the morphology and geographical distribution of the rush, together with some observations on its ecology in its British habitat and in the Mediterranean. Some of this information was given at the Society's Exhibition meeting in November 1958, when herbarium specimens of the Berrow plant were shown.

MORPHOLOGY AND TAXONOMY

J. subulatus was described by Forskål (1775) in *Flora Aegyptiaco-Arabica*, and later Desfontaines (1798) described it under the name *J. multiflorus* (non *J. multiflorus* Retz., 1795). Buchenau (1890, 1906) classified *J. subulatus* as the only member of the subgenus *Junci subulati*; the subulate stem leaves, some of which are inserted high on the axis, are an important diagnostic character.

The British *J. subulatus* seems to be very similar to the Mediterranean plant. It has a strong, slightly branched rhizome which creeps c. 6 cm. (4–8 cm.) below the mud surface and is about 6 mm. in diameter. The rhizome bears brown scale-leaves (see Fig. 1 A) and buds which give rise to rather fragile erect aerial shoots, 2–10 cm. apart. These are often a metre or more high and 3–4 mm. in diameter at the base where they bear several shiny brown sheaths. The stems, which are furrowed and in the autumn vinous red at their bases, bear two to four leaves which are somewhat channelled, non-articulate and hollow except for evanescent web-like partitions (Buchenau, 1906, p. 102), as in the stem. The leaves have sheathing bases (c. 10 cm.) and pronounced ligules (Fig. 1 B), and like the stems are glaucous grey-green during the growing season.

The inflorescence is many-flowered, interrupted, diffuse, and subtended by a short bract. The pale yellowish-green flowers are about 3.5 mm. long, cup-shaped at first (Fig. 1 C) and later spreading; each is surrounded by membranous, acute bracteoles with broad bases (Fig. 1 G). The outer perianth segments are lanceolate, acute, and rather longer than the inner, which are more obtuse and slightly involute with a fairly broad subterminal portion, having whitish membranous margins (Fig. 1, E & F). Inserted close to the perianth are the six stamens with short filaments and anthers c. 1 mm. long.

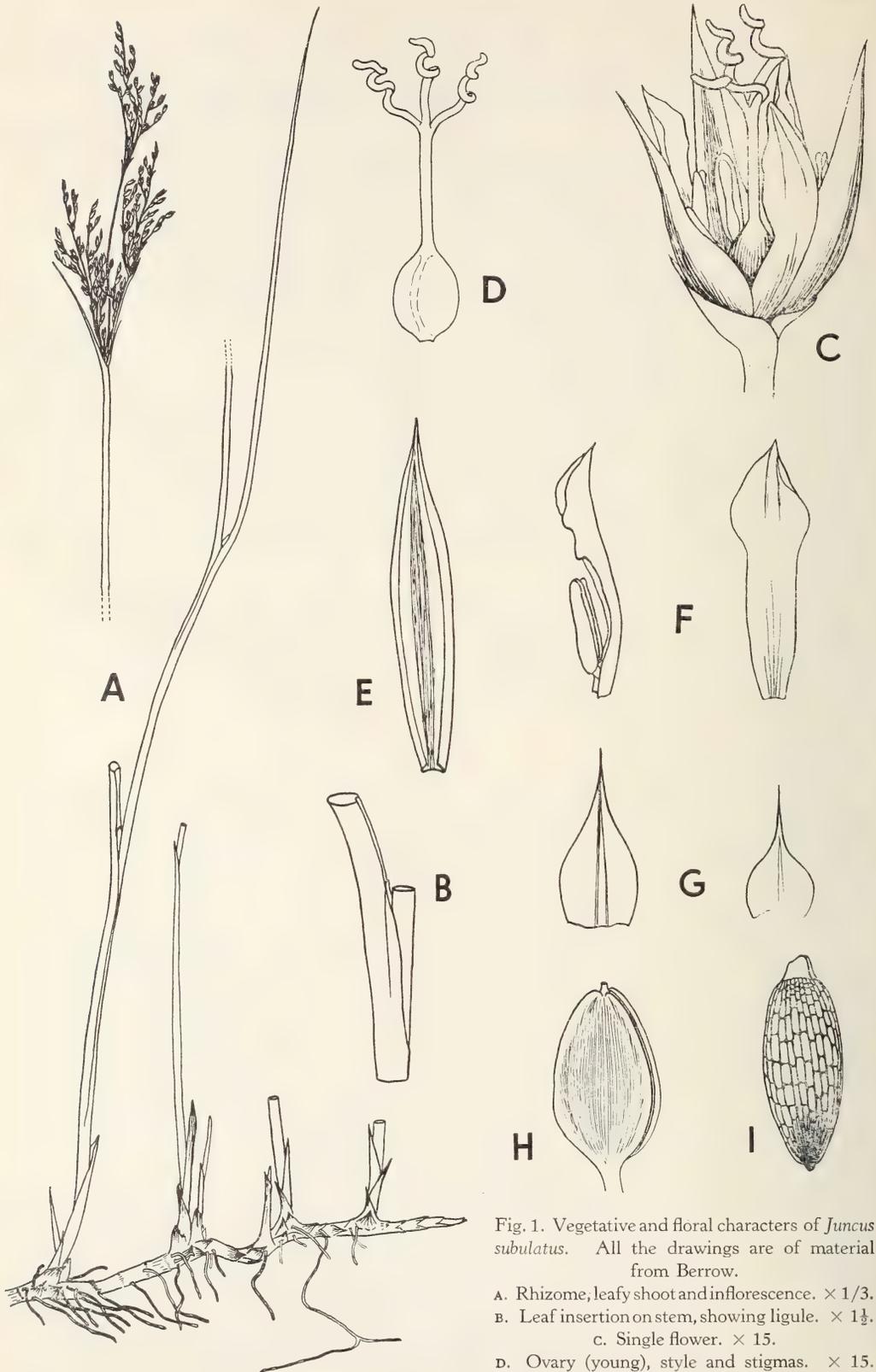


Fig. 1. Vegetative and floral characters of *Juncus subulatus*. All the drawings are of material from Berrow.

A. Rhizome, leafy shoot and inflorescence. $\times 1/3$.

B. Leaf insertion on stem, showing ligule. $\times 1\frac{1}{2}$.

C. Single flower. $\times 15$.

D. Ovary (young), style and stigmas. $\times 15$.

E. Outer perianth segment, ventral view. $\times 18$.

F. Inner perianth segment, lateral view (with stamen) and ventral view. $\times 18$.

G. Bracteoles. $\times 18$.

H. Capsule, fairly mature. $\times 15$. I. Seed. $\times 40$.

The unilocular ovary later becomes almost completely trilocular by the ingrowth of septa, and bears the style (c. 1 mm.) with three pink papillose stigmas which twist clockwise, as seen from above (Fig. 1 D). The mature capsule is trigonous (Fig. 1 H), usually a little shorter than the perianth, shiny reddish-brown, and often mucronate (cf. Fiori & Paoletti, 1921, p. 74). Only a few (2–5) of the numerous ovules mature and the longitudinally reticulate seeds are 0.6–1.0 mm. long and slightly appendaged (Fig. 1 I).

Herbarium material indicates that *J. subulatus* varies little over its range. Cosson and Durieu, however, described a more slender plant under *J. multiflorus* Desf. subvar. *salinus* from Algeria (Bory de St. Vincent *et al.*, 1854–67). The name for this plant is now *J. subulatus* f. *salinus* (Dur.) Maire & Weiller (Maire & Weiller, 1957); it is smaller than the Berrow rush, has narrower leaves, and a less-branched inflorescence.

GEOGRAPHICAL DISTRIBUTION

The chief area of distribution of *J. subulatus* is the Mediterranean (Fig. 2), but the plant also occurs in the region of the Caspian Sea (Täckholm & Drar, 1950; Maire & Weiller, 1957). Information about the latter area is, however, so limited that here attention will be confined to the former. The data on Fig. 2 were compiled from the herbaria of the British Museum, the Royal Botanic Gardens, Kew, the University of Bristol, and various Floras (see references).

J. subulatus is usually a maritime species. It occurs locally around the Mediterranean and on many of the islands, mostly in salt marshes not far from the sea. Records are most abundant from North Africa, and the centre of its distribution is almost certainly in the Nile Delta region of Egypt, where it is especially abundant between Port Said and Alexandria; it extends southwards up the Nile as far as Asyut (Täckholm & Drar, 1950). *J. subulatus* is also found at a number of oases inland, especially in the Kharga and Bahariya regions west of the Nile. The plant is recorded for the fresh water canal at Port Said, and appears able to survive in non-saline habitats (see also Maire & Weiller, 1957). From Egypt the rush extends westwards along the coast of North Africa, occurring locally as far as Morocco, inland in the Ahaggar region of the Sahara, and at high altitudes in the shotts of the Algerian plateaux (Braun-Blanquet, 1932, p. 197). *J. subulatus* also occurs locally all along the northern Mediterranean shores from Syria and Turkey to Spain. Of special interest is its occurrence at two places on the Atlantic coast of Spain (at Bilbao, and near Oviedo) suggesting a similar distribution to that of certain 'Lusitanian' and south-western rarities of our British flora, which also appear to reach their northern limit in south-west England or Ireland. Examples are *Scirpus holoschoenus*, *Helianthemum apenninum*, *Juncus pygmaeus*, and *Asplenium adiantum-nigrum* subsp. *onopteris*; the first is in some respects ecologically similar to *J. subulatus* but its distribution is more continental and extends into Siberia, while the last three show a closely similar geographical pattern in spite of their very varied ecology.

ECOLOGY

(a) *The British Isles*

The Berrow salt marsh is of recent origin and has developed between the channel of the river Parrett and the sand dune system inland. Colonisation of the marsh began in 1910 and may have been made possible by the formation of a new tributary channel draining from the muddy Berrow flats into the Parrett. Vegetation was sparse until 1920, when the commonest plants were *Salicornia* spp. and *Puccinellia maritima* (Thompson, 1922). *Spartina townsendii*, which was first noticed in 1920, now dominates much of the

area, and *Salicornia* spp. have much declined. The marsh has doubtless risen gradually by mud and sand accretion and is now separated from the open shore by a broken ridge of low embryo dunes, formed in the last twenty years (Kendall, 1938). It is partially flooded by sea water only at very high tides; some fresh water drains into it by seepage from the dunes which form the landward boundary.

The vegetation of the marsh clearly falls into three zones. A belt transect of the marsh was surveyed in August 1958, the vegetation being scored by the technique of

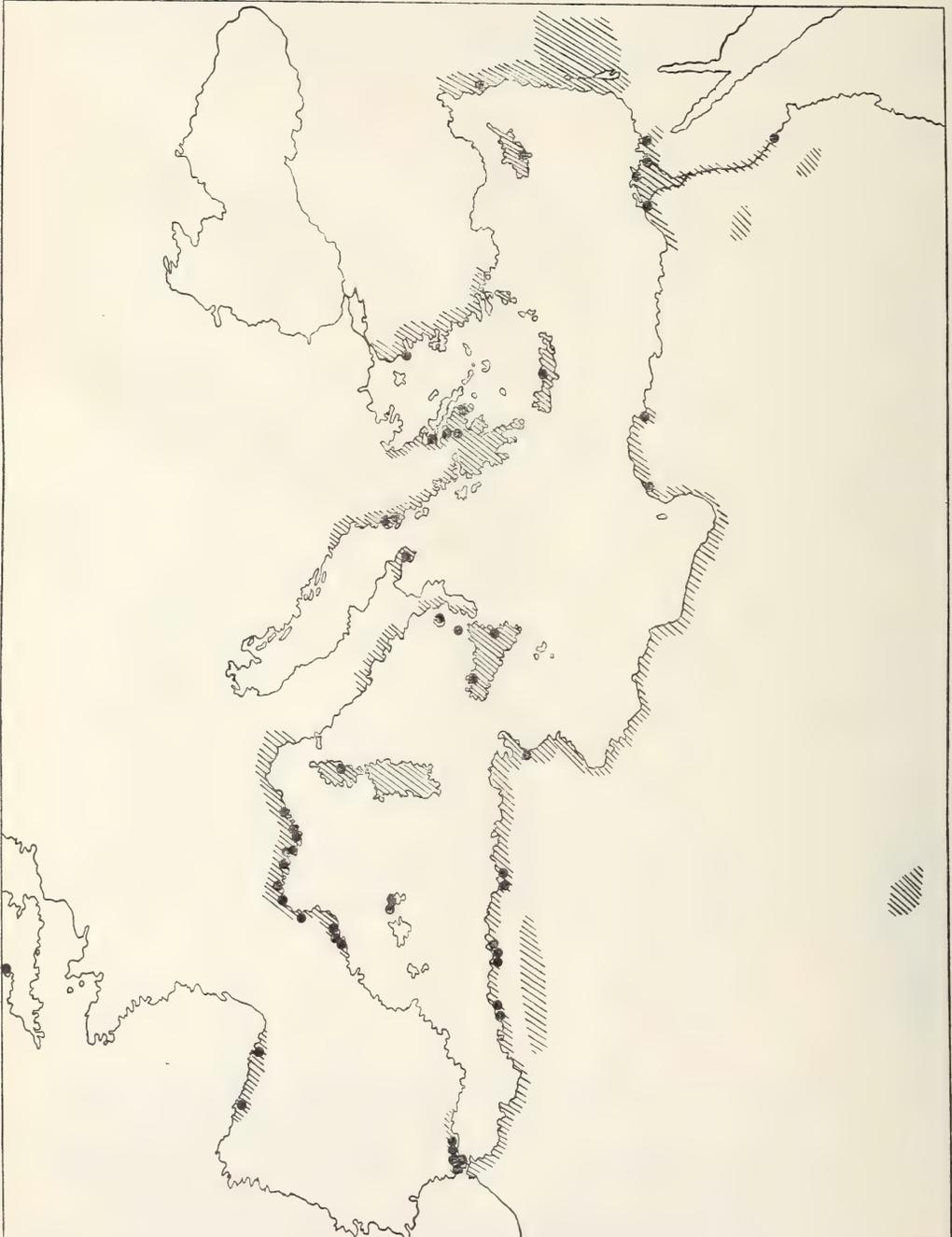


Fig. 2. The geographical distribution of *J. subulatus*; the occurrence of the plant in the Caspian Sea region is not included. Records based on herbarium specimens are shown by ●; information on distribution derived from Floras is indicated by hatching.

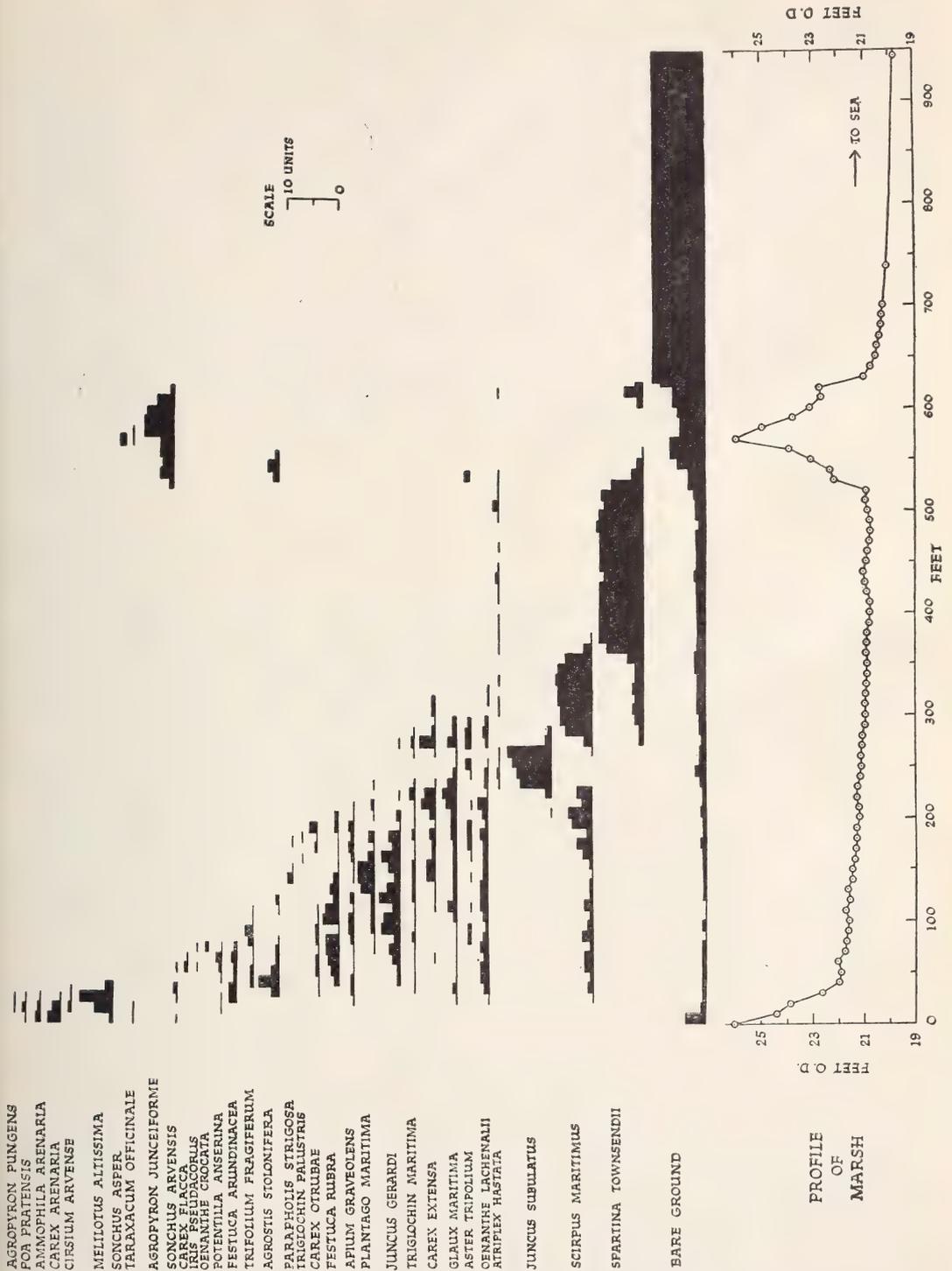


Fig. 3. The profile and vegetation of a transect across the marsh at Berrow, mid-August 1958. The vegetation was scored (out of 10 units) according to the relative bulk (volume) of the component species, an allowance for bare ground being made; successive areas, 10 feet long and 3 feet wide, along the transect were recorded. The distribution of most of the plants is shown in histogram form, but not included in the figure are the following: distance 0-10ft., 0.5 unit of *Bromus mollis*, *Calystegia soldanella*, 0.1 unit of *Cerastium holosteoides*, *Crepis capillaris*, *Holcus lanatus*, *Hypochaeris radicata*, *Senecio jacobaea*, *Trifolium arvense*, *T. campestre*; 10-20ft., 0.5 unit of *Bromus mollis*, *Trifolium repens*, 0.1 unit of *Crepis capillaris*, *Holcus lanatus*, *Plantago major*, *Poa annua*, *Ranunculus acris*, *Trifolium arvense*, *T. campestre*, *Vicia angustifolia*; 20-30ft., 0.1 unit of *Bryum pseudotriquetrum*, *Lycopus europaeus*.

Willis *et al.* (1959); the results are given in Fig. 3, which shows that the slope of the marsh is fairly uniform. The lowest area, to seaward, is dominated by *Spartina townsendii*, and few other plants are able to survive its competition. In the next zone *Scirpus maritimus* is very abundant; it is here that *J. subulatus* occurs and is clearly dominant in the two patches where it grows. Both patches are at closely similar levels (21.1 and 21.4 ft. O.D.). In the third zone, at still higher levels, a number of species dominate locally; *Juncus gerardii*, *Oenanthe lachenalii*, *Festuca rubra*, *Carex extensa*, *Plantago maritima* and *Glaux maritima* are plentiful. The presence of *Iris pseudacorus*, *Phragmites communis* and *Typha latifolia* on the landward margin of the zone suggest the influence of fresh water here.

J. subulatus is clearly subject to considerable changes of salinity at Berrow, since the sites are reached by only the highest tides. The rush is known to tolerate high concentrations of salt (Braun-Blanquet, 1932, p. 193) and at Berrow must at times be growing under conditions of low salinity. Measurements of the sodium chloride content of the soil water (using a flame photometer) after a period of fairly high tides in December, 1958, gave a value of 1.0% at the seaward margin of the colony shown in Fig. 3. At the inland limit of this colony the sodium chloride content was 0.9%, and of the second, which is further inland, 0.7%. The calcium content of the soil water was low (0.01–0.02%) and the pH between 7.2 and 7.5.

(b) *The Mediterranean*

J. subulatus often grows bordering brackish lagoons in southern France and its main association is *Salicornietum fruticosae* (Braun-Blanquet, 1952); frequently occurring with the rush are *Salicornia fruticosa*, *S. radicans*, *Arthrocnemum glaucum*, *Puccinellia convoluta*, *Triglochin bulbosa*, *Halimione portulacoides*, *Limonium vulgare*, *Suaeda maritima*, *Aeluropus littoralis*, and *Polypogon maritimus*. With the last two grasses *J. subulatus* forms a sub-association succeeding *Salicornietum* after burning, which destroys *Salicornia*, whereas the *Juncus* rhizomes survive. Near the mouths of the Rhône, the rush, sometimes accompanied by *Juncus maritimus*, dominates areas less saline than those occupied by *Salicornia* spp., but the *Juncetum* may be progressively invaded by *Phragmites communis* as the salt content of the soil diminishes (Molinier, 1948).

In Spain the rush often occurs with *Salicornia* spp. in littoral calcareous marshes (A. & O. Bolós, 1950); the commonest associates are *Scirpus maritimus*, *Eleocharis palustris* and *Juncus maritimus*. Another somewhat similar community is described by Holmboe (1914, p. 211–2) from Cyprus; here, in a brackish lagoon, its associates included *J. acutus*, *Scirpus maritimus*, *Carex divisa* and *Triglochin bulbosa*.

OCCURRENCE AND CLIMATIC LIMITATION IN BRITAIN

J. subulatus must be regarded as a recent arrival, since its only known locality in Britain has not long been vegetated. It seems likely that the rush was brought in by shipping or birds from the Mediterranean, and was carried by tidal action to the site where it is now flourishing.

At Berrow *J. subulatus* is at its northern limit of distribution (see Fig. 2), and its flowering season is much later than in the Mediterranean. In North Africa and Syria it flowers between April and July, and fruits from July onwards, whereas at Berrow and in the Bristol University gardens it flowers from July or August to September and fruits correspondingly later, if at all. The fruiting at Berrow seems to depend on a warm dry summer; in the wet autumn of 1958 only little seed was set, although plants grown in a greenhouse produced some good fruits and seeds in late September. Possibly the northern

extension of the plant is controlled more by the length and temperature of the growing season than by the low temperature of winter, the rush in this respect perhaps showing a parallel to *Scirpus holoschoenus* (Willis, unpublished). The amount of rainfall in summer may well have an important effect on the fruiting of *J. subulatus*.

Although the plant may not often produce viable seed at Berrow, it is spreading sufficiently vigorously by the growth of the rhizome to replace *Scirpus maritimus*, and gives every appearance of becoming an important member of the salt marsh community.

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* Used in compilation of Fig. 2.

[Note added in proof. The two colonies have now been recognised on aerial photographs in April, 1954.]

GENTIANELLA IN BRITAIN

II. *GENTIANELLA SEPTENTRIONALIS* (DRUCE) E. F. WARB.

By N. M. PRITCHARD

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SUMMARY

Discriminant analysis as a taxonomic tool is used at subspecific level to investigate the variation within *G. septentrionalis*. It reveals morphological differences and geographical discontinuity between two groups, an eastern and a western group. The differences between these groups are of a similar order to those between *G. amarella* and *G. septentrionalis*, and the new taxa are described as subspecies of *G. amarella*; *G. amarella* subsp. *septentrionalis* (Druce) Pritchard and subsp. *druceana* Pritchard. Local variation within each subspecies suggests the existence of regional races, similar to those described for *G. amarella* subsp. *amarella* in an earlier paper.

ECOLOGY AND DISTRIBUTION

G. septentrionalis occurs in similar habitats to those of *G. amarella*, that is in grassland on dunes and calcareous rock. The dunes are invariably those containing a high proportion of calcareous shell-sand, while only on limestone does the plant occur inland. Thus *G. septentrionalis* appears to be even more markedly calcicolous than *G. amarella*. The two plants are similar in their preference for open habitats, though *G. septentrionalis* is frequently found on young dunes, often in association with healthy *Ammophila*.

G. septentrionalis is probably endemic in Scotland, although plants collected by Whitehead in Iceland bear certain similarities to the Scottish plants. This point must for the time being remain doubtful, since there is no evidence of the flower colour of the Icelandic plants. It is found only in Perth, Angus and possibly Aberdeen on limestone, and in Ross, Sutherland, Caithness, Orkney, Shetland and Lewis on limestone and on dunes. It thus replaces *G. amarella* geographically in the northern half of Scotland, and the two plants are not found together.

Among the most frequent associates of *G. septentrionalis* are *Achillea millefolium*, *Agrostis stolonifera*, *Carex flacca*, *Euphrasia* spp., *Festuca* spp., *Galium verum*, *Linum catharticum*, *Lotus corniculatus*, *Plantago* spp., *Prunella vulgaris*, *Thymus drucei*, *Trifolium repens* and *Viola canina*.

BIOMETRIC WORK

A preliminary examination of a wide range of herbarium material indicated considerable variation in a number of morphological characters. These differences are of the same general order as those already discussed for other members of the *G. amarella* aggregate in an earlier paper (Pritchard, 1959).

G. septentrionalis has in recent years been regarded as a single species. A certain amount of variation appears to have been recognised, since plants from certain parts of its range have been placed in the varieties *calycinæ* and *multicaulis*. (The taxonomic history of the species is complicated, and is discussed later). The problem could be defined thus. First, have these varieties anything but purely local significance, and secondly does the total range of variation show any ecological or geographical correlations?

From the initial examination of the herbarium specimens and also of a number of random samples collected in various parts of the species range, the following 5 characters were found to be the most valuable.

- (1) Number of internodes.
- (2) Degree of contraction of the terminal internode. For reasons earlier discussed, this is treated in the form $(\text{Log } \frac{\text{Average}}{\text{Terminal}} \text{ Internode}) + 1$ (Internode Ratio).
- (3) and (4) Leaf shape. The same two formulae as before were used, that is
 - (3) Leaf $\frac{\text{Length}}{\text{Width}}$
 - (4) Leaf $\frac{B - A}{2 \times \text{length}} \times 100$ (Leaf-taper Index).
- (5) Inequality of the calyx, expressed in the form

$$\text{Calyx } \frac{\text{longest}}{\text{shortest}} \text{ arms (Calyx-tooth Ratio).}$$

A number of other characters, while not so useful, afforded confirmation of the conclusions reached in some cases. In Table 1 the means, standard deviations and standard errors of the mean are given for the following four random samples and five non-random samples selected from fairly large herbarium gatherings from geographically intermediate localities.

Random samples :	<i>National grid reference</i>
444 Tomphubil Quarry, Perthshire	NN 7754
445 Duncansby Head, Caithness	ND 4073
446 Dunnet Links, Caithness	ND 2169
448 Coll, Stornoway, Lewis	NB 4638
Non-random samples :	
SH Schiehallion, Perthshire	NN 7154
DL Dunnet Links, Caithness	ND 2169
RY Reay, Caithness	NC 9664
ID Inchnadamph, W. Sutherland	NC 2522
MC Mellon Charles, W. Ross	NG 8491

TABLE 1
Statistical data for 4 random and 5 non-random samples

Sample	No. of plants	No. of Internodes			Internode Ratio			Leaf L/W			Leaf-taper Index			Calyx-tooth Ratio		
		\bar{x}	σ	SEM	\bar{x}	σ	SEM	\bar{x}	σ	SEM	\bar{x}	σ	SEM	\bar{x}	σ	SEM
444	44	2.50	0.63	0.10	1.06	0.17	0.03	3.83	0.98	0.14	5.40	3.75	0.53	1.30	0.21	0.03
445	37	3.08	0.67	0.11	1.16	0.15	0.03	3.26	0.66	0.11	5.53	2.73	0.45	1.11	0.16	0.03
446	38	3.63	0.95	0.16	1.16	0.24	0.04	3.85	0.81	0.13	6.33	2.61	0.42	1.19	0.13	0.02
448	25	5.40	0.90	0.18	1.48	0.31	0.06	2.46	0.32	0.07	12.20	1.95	0.39	1.53	0.34	0.07
SH	8	3.87	1.17	0.42	1.16	0.17	0.06	3.88	0.76	0.27	5.38	1.11	0.39	1.21	0.11	0.04
DL	9	3.78	0.63	0.21	1.05	0.15	0.05	2.63	0.55	0.20	8.25	2.64	0.94	1.22	0.16	0.06
RY	10	3.60	0.92	0.29	0.97	0.12	0.04	4.12	0.84	0.27	5.50	2.34	0.74	1.21	0.19	0.06
ID	9	4.56	0.83	0.28	1.28	0.22	0.08	2.84	0.43	0.15	12.89	2.73	0.91	1.46	0.14	0.09
MC	15	5.53	1.43	0.35	1.51	0.28	0.07	2.89	0.44	0.11	11.72	1.90	0.46	1.52	0.24	0.06

The figures in Table 1 indicate a considerable range of variation between the samples, although for the most part the individual samples are relatively uniform. Among the four

random samples it can be seen that while 444, 445 and 446 lie fairly close together, in all the five characters 448 is rather different. The results of *t* tests carried out among the four samples confirm this, and are summarised in Table 2. In all five characters examined, 448 differs significantly at the $p < 0.001$ level from its nearest neighbour.

TABLE 2
Results of "t" tests in four random samples.

		445	446	448
444 and :	<i>No. of Internodes</i>	$p < 0.001$		
	<i>Internode Ratio</i>	$p < 0.02$	$p > 0.05$	
	<i>Lf. L/W</i>	$p < 0.001$		
	<i>Calyx-tooth Ratio</i>		$p < 0.001$	$p < 0.001$
445 and :	<i>No. of Internodes</i>		$p < 0.01$	
	<i>Internode Ratio</i>		$p > 0.5$	$p < 0.001$
	<i>Lf. L/W</i>			$p < 0.001$
	<i>Leaf-taper Index</i>		$p > 0.8$	
446 and :	<i>Calyx-tooth Ratio</i>		$p < 0.02$	
	<i>No. of Internodes</i>			$p < 0.001$
	<i>Leaf-taper Index</i>			$p < 0.001$

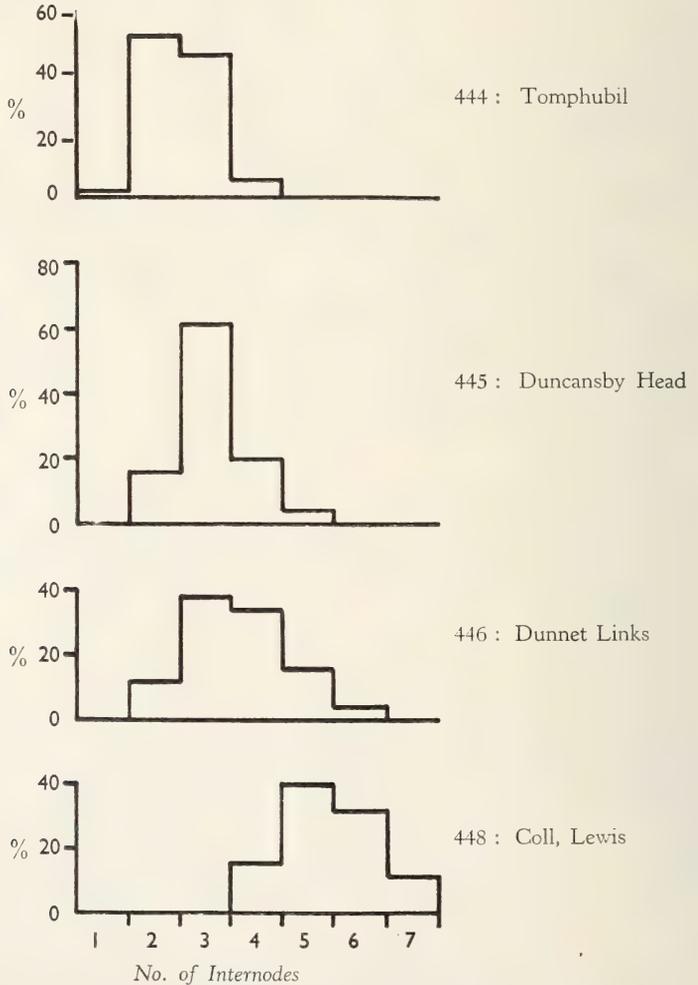


Fig. 1. Four random samples : Number of Internodes.

No one of the characters used can be employed to separate 448 clearly from the other three samples. Figs. 1 and 2 show, for example, the distribution of two of the characters, Number of Internodes and Leaf-taper Index. If the characters are combined in pairs the distinction is clear between 448 and the other three samples. Figs. 3 and 4 show the combinations of Number of Internodes with Leaf Length/Width and of Calyx-tooth Ratio with Internode Ratio. In these figures the crossbars represent extensions of twice the standard error of the mean on each side of the mean. Despite the inequality of the sample sizes, this gives a very rough estimate of the significance of the difference between the samples.

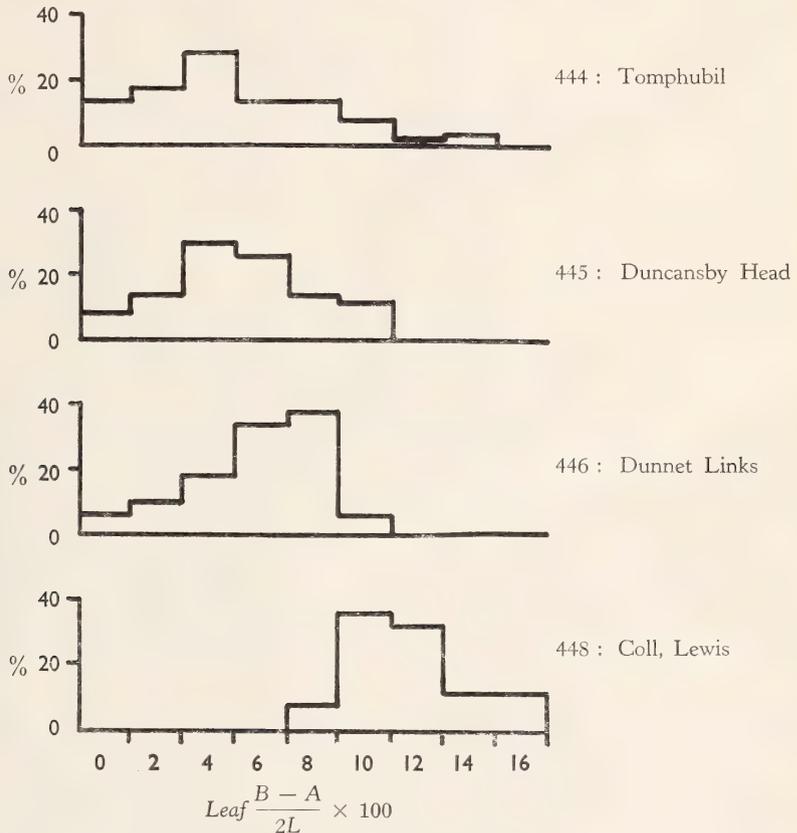


Fig. 2. Four random samples : Leaf-taper Index.

TABLE 3. Samples arranged in order of magnitude for each of five characters.

(1) No. of Internodes	(2) Internode Ratio	(3) Leaf L/W	(4) Leaf-taper Index	(5) Calyx-tooth Ratio
444	RY	RY	SH	445
445	DL	SH	444	446
RY	444	446	RY	RY
446	446	444	445	SH
DL	SH	445	446	DL
SH	445	MC	DL	444
ID	ID	ID	MC	ID
448	448	DL	448	MC
MC	MC	448	ID	448

The differences might be accounted for in a number of ways. The only marked ecological differences are between 444, an inland limestone sample, and the other three. There is no apparent difference between the habitats of 448 and the other dune samples, 445 and 446. However, 448 comes from Lewis, an island separated from the Scottish mainland by about 50 miles. The results of this isolation are difficult to assess, but considerable morphological differences might be expected.

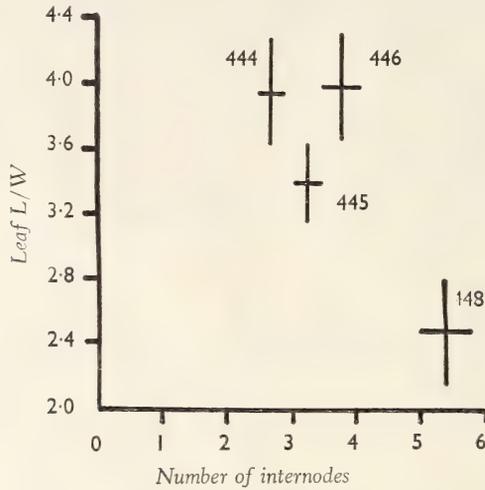


Fig. 3. Correlation of Number of Internodes with Leaf L/W.

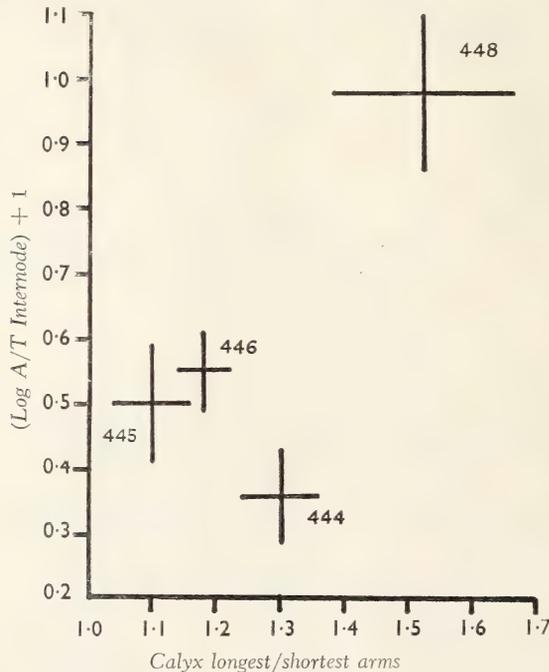


Fig. 4. Correlation of Calyx-tooth Ratio with Internode Ratio.

Table 3 is an arrangement of the four random and five non-random samples in order of magnitude for the five characters. In all these lists, with the exception of Leaf Length/

Width, the plants from Tomphubil, Schiehallion, Duncansby Head, Dunnet Links and Reay come at one end of the list, and those from Inchnadamph, Mellon Charles and Coll at the other, although the orders vary within these two groups. In the exception the unusually broad leaves of the plants from Dunnet Links (DL) place them among the second group.

Although a possible grouping is suggested by these arrangements (i.e. into an eastern and a western group) no single character suffices to separate the two groups. A preliminary summary of the data was obtained by allocating arbitrary scores of 1 or 2 points for each character and plant; the division of the ranges of data is shown in Table 4. The scores

TABLE 4
Allocation of points for each character

Character	1 point	2 points
No. of internodes	1-4	5-7
Internode ratio	0.70-1.29	1.30-2.30
Leaf L/W	3.10-7.00	1.95-3.09
Leaf-taper index	0-10.4	10.5-16.0
Calyx-tooth ratio	1.00-1.35	1.36-3.00

for each plant are added, and the resultant distributions of scores are shown in Figure 5. From the histograms it is clear that the samples from Coll, Mellon Charles and Inchnadamph are distinct from the other six samples. Figure 6 shows the results of combining the histograms of Figure 5 into two groups, one eastern and one western. Although the distinction is clear, an overlap of about 12% still occurs.

The preliminary hypothesis is that two groups (or possibly a cline) can be distinguished within *G. septentrionalis*, one eastern (Group E) and one western (Group W). No single character exists which can be used to separate the two groups, and an expression is required such that individual plants may be clearly distinguished as members of one or other group.

The work of Whitehead (1954, 1955-6) on *Cerastium* sect. *Viscosa* is interesting in that the situation there bears some resemblance to that in *G. septentrionalis*. There appear to be distinct groups whose separation by eye on one or two characters is not possible in a substantial proportion of the specimens. Accordingly, the method of discriminant analysis has been examined and applied to the situation in *G. septentrionalis*. The history of the use of discriminant analysis as a tool in plant taxonomy is discussed at length by Whitehead (1948) and is not repeated here. Some justification for the method is, however, required.

The division of each character's range into two parts has already been examined and found wanting, although in some cases it may be quite adequate. In that each character is given the same arbitrary value in discrimination it represents, in fact, a false weighting of the evidence in a purely subjective manner. For the same reasons, multiplication of the values by a constant factor for any "useful" character is normally to be rejected. By this type of weighting, complete discrimination for the samples considered can always eventually be obtained. The same weightings can hardly be relied upon to include discrimination among new specimens, since they may bear little or no relation to the variation within and between the groups treated.

A more accurate method would be to divide the total range into a larger number of parts (say 100) and to sum the values for each plant. This is, of course, subject to the same criticisms in that each character is given equal weight. It may reveal, on the other

hand, correlations within the groups not previously noticed, and thus strengthen the discrimination. When this is done for *G. septentrionalis*, the curve obtained is bimodal with modes at about 180 – 200 and 280 – 300, with considerable overlap. If the specimens are divided by eye into two groups, and the means of the total scores calculated, they are found to be 199 (Group E) and 305 (Group W). The distribution of total scores thus represents a difference in the populations, although the overlap is still too large for any specimen to be allocated with a reasonable degree of certainty (the chances of misplacement are about 1 in 4).

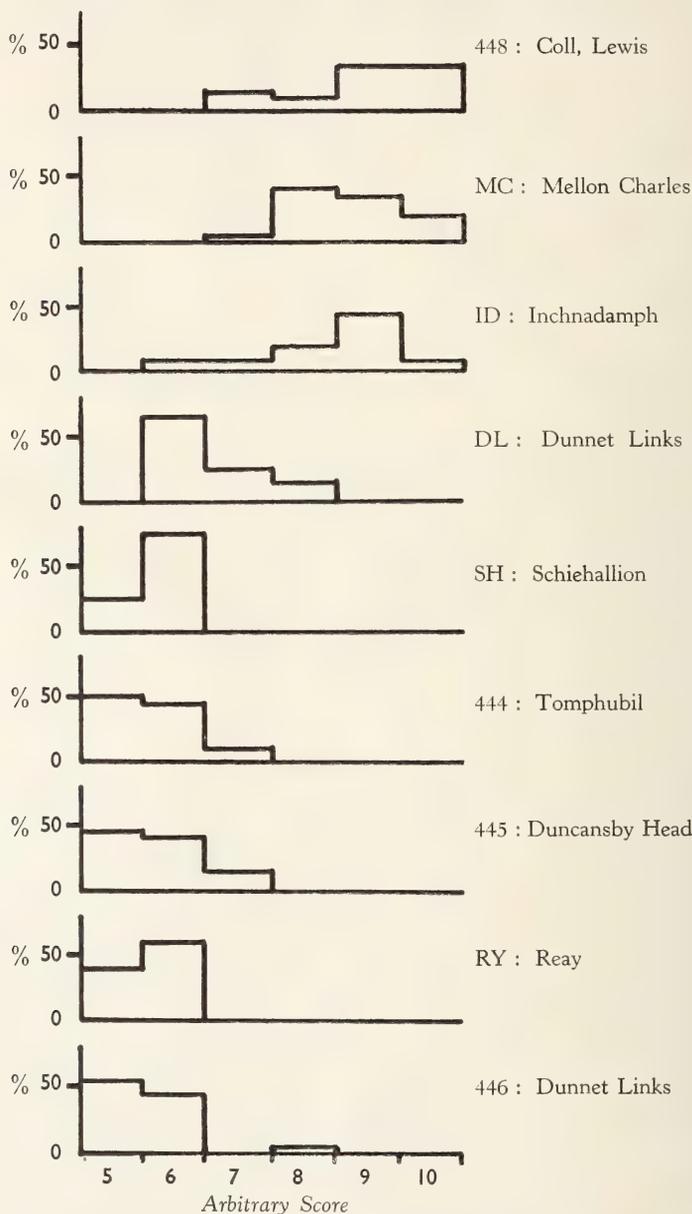


Fig. 5. Four random and five non-random samples : Distribution of arbitrary scores.

Discriminant analysis is a method of weighting each character in such a way that the weighting is conditioned by the actual patterns of variation within and between the

groups. If we have two types, taxa, racial groups or collections of organisms or data, then the discriminant function may be defined as a linear compound of all the available measurements which will give the smallest frequency of misclassification when used to separate the two groups.

The statistical theories involved in the method are described by Fisher (1941) but they are difficult to follow for non-statisticians. The method has been applied in taxonomic problems by Fisher, Melville (1950), Whitehead and others. Its application here is essentially similar to that of Whitehead, and the details are not described.

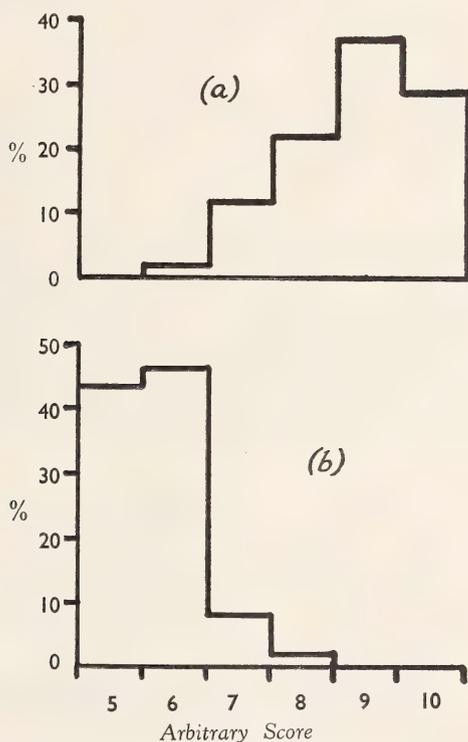


Fig. 6. Combinations of data from Fig. 5 :
 (a) Western (448, ID and MC),
 (b) Eastern (444, 445, 446, DL, RY and SH).

The aim of the method is to divide a patently heterogeneous species *G. septentrionalis*, into two discrete taxa.

The first stage is to obtain measurements for the 5 characters used in the analysis for each plant. These characters have already been described. For the later stages of the analysis it is necessary to separate the specimens into two groups by eye. Since no previous information existed, this was done by comparison with the four random samples 444, 445, 446 and 448. Those most closely resembling 444, 445 and 446 were placed in one group, those most like 448 in the other. Each specimen received a reference number. Subsequent treatment of the data followed the pattern described by Whitehead. The eventual weighting factors obtained for the five characters appear in Table 5.

TABLE 5
Weighting factors

No. of Internodes	+ 212.7125
Internode Ratio	+ 141.2634
Leaf L/W	+ 123.0802
Leaf-taper Index	- 25.5390
Calyx-tooth Ratio	+ 254.1575

Thus, since the discriminant function (F) is the best linear function for discriminating between Group E and Group W, the sum of the mean values of each character multiplied by the appropriate weighting factor will give the discriminant function. On the original separation by eye the values of this function are :

$$\begin{aligned} \text{Group E; } F &= 24,867 \\ \text{Group W; } F &= 42,044 \end{aligned}$$

The point of delimitation between groups will be the mean of these two values, and is 33,456.

If there has been complete discrimination, then any plant whose value lies below 33,456 will belong to group E and any whose value is above this to Group W. The histogram obtained for the whole range of (F), calculated using the approximate values $\lambda_1 = 213$, $\lambda_2 = 141$, $\lambda_3 = 123$, $\lambda_4 = -26$ and $\lambda_5 = 254$, shows that complete separation has not been obtained (Fig. 7). Figure 8 shows the distribution of (F) for the two groups separately. If the calculated midpoint is taken for convenience at the 33,000 mark on the histograms, then the overlap consists of about 11% of all the plants.

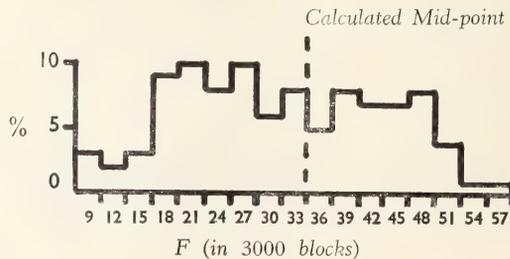


Fig. 7. Distribution of F for all specimens.

The 22 plants comprising this 11% are listed in Table 6, together with their values of (F) and geographical localities. They are all those plants of group E whose (F) exceeds 33,456, and all those of Group W whose (F) is less than 33,456.

The significance of these is purely subjective, since the primary division into groups E and W in which these 22 plants appear to be misplaced was itself subjective. Nevertheless, they show a number of points of interest.

- (1) Specimens E14 and E15 (whose deviations from 33,456 are only 1,366 and 206 respectively) are part of the random sample 446. E14 has an unusually high value for the Internode Ratio (1.37), combined with an above average number of internodes, 5. E15 has 6 internodes, one more than any other member of Group E, and in both specimens these factors account for the high F . However, they must clearly be retained in group E.
- (2) Specimen L22 is part of random sample 448, and its deviation from 33,456 is only

TABLE 6
Overlapping samples.

No.	Locality	v.c.	Nat. Grid Ref.	F
E14	Dunnet Links	109	ND 16	34,822
E15	Dunnet Links	109	ND 16	33,667
E52	Felar	112	HU 69	34,557
E67	Spiggie	112	HU 31	37,148
E68	Spiggie	112	HU 31	39,984
E92	Quendale	112	HU 31	48,946
E93	Quendale	112	HU 31	35,423
E94	Spiggie	112	HU 31	34,221
E96	Spiggie	112	HU 31	39,793
E97	Spiggie	112	HU 31	38,434
L22	Coll	110	NB 43	32,294
L29	Tongue	108	NC 55	30,554
L32	Burrafirth	112	HP 61	32,608
L34	Burrafirth	112	HP 61	21,280
L39	Tongue	108	NC 55	23,686
L44	Sumburgh	112	HU 40	26,623
L61	Bettyhill	108	NC 76	21,360
L66	Inchnadamph	108	NC 22	29,976
L70	Inchnadamph	108	NC 22	28,385
L74	Durness	108	NC 46	30,717
L85	Burrafirth	112	HP 61	15,092
L89	Burrafirth	112	HP 61	31,618

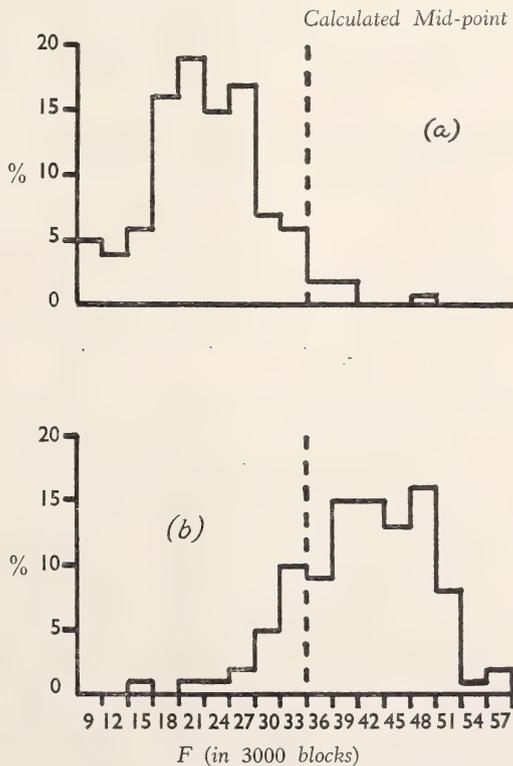


Fig. 8. Distributions of F for (a) Eastern and (b) Western groups.

1,162. Both the number of internodes (4) and the Internode Ratio (1.06) are below average for group W, but the plant must remain in that group.

(3) Specimens L29, L39, are L61 and from very near the point of demarcation between groups E and W (which lies in the Tongue-Bettyhill area) and are considered later.

(4) Specimens L66 and L70. In L66 there are only 3 internodes. This is coupled with a low value for the Internode Ratio (1.01). L70 has 4 internodes, coupled with a subequal-armed calyx.

(5) L74 has unusually long and narrow leaves, which reduce its value for leaf-taper index to 8.33.

In no case does the deviation from 33,451 exceed 5,000 and from a comparison of the histograms above we may regard this as falling within the area of variation of (F) for each group.

Mean of group E = 24,857

Standard deviation of E = 5,820

Mean_E + 3 × standard deviation_E = 42,317

This area (plus its equivalent Mean - 3 × standard deviation) should contain theoretically 99.7% of group E. It does in fact do so.

Mean of group W = 42,044

Standard deviation of W = 6,480

Mean_W - 3 × standard deviation_W = 22,604

This area (plus its equivalent Mean + 3 × standard deviation) should contain theoretically 99.7% of group W. It does in fact do so.

(6) Specimens E52, 67, 68, 93, 94, 96, 97, L32, 34, 44, 85 and 89 are all from Shetland, and they represent 59% of the total number of plants misclassified by eye. Since there were only 38 Shetland plants in the original analysis, they also reveal that of these no less than 34% were misclassified, as against only 6% misclassification of the mainland plants.

It is now desirable to look more closely at the variation of Shetland plants. For this purpose, a visit was made to Shetland in August 1956, and random samples from a number of populations made. These were :-

		National grid reference
479	S. Ninian's Isle	HU 3621
480	Spiggie	HU 3717
481	Quendale	HU 3713
482	Sumburgh	HU 4009
483	Sumburgh	HU 4009

The statistical data for these populations are given in Table 7.

TABLE 7
Statistical data for Shetland plants

Character	480 (46 plants)			481 (29 plants)			482 (9 plants)			483 (19 plants)		
	\bar{x}	σ	SEM	\bar{x}	σ	SEM	\bar{x}	σ	SEM	\bar{x}	σ	SEM
1. No. of Internodes	3.76	0.96	0.14	4.97	0.72	0.13	5.22	0.62	0.21	4.32	0.80	0.18
2. Internode Ratio	1.10	0.29	0.04	1.01	0.20	0.04	1.22	0.13	0.04	1.08	0.16	0.04
3. Leaf L/W	2.59	0.48	0.07	2.61	0.51	0.09	2.73	0.33	0.11	2.51	0.46	0.11
4. Leaf-taper Index	12.26	3.57	0.53	12.66	3.02	0.56	11.00	1.89	0.63	11.89	4.10	0.94
5. Calyx-tooth Ratio	1.39	0.23	0.03	1.42	0.24	0.04	1.21	0.30	0.10	1.43	0.29	0.07

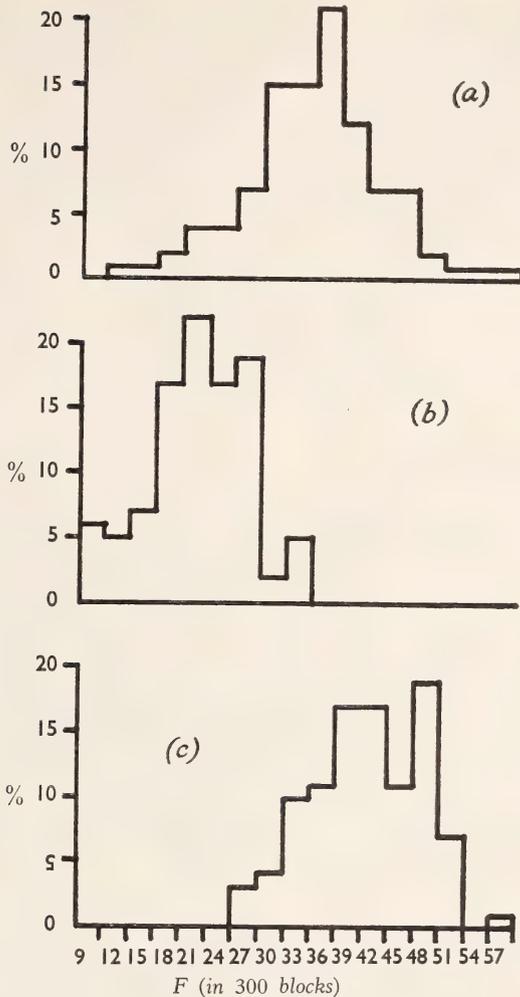


Fig. 9. Distributions of F for :
 (a) All Shetland plants,
 (b) Eastern group excluding Shetland plants, and
 (c) Western group excluding Shetland plants.

(1) *Number of Internodes*. The values are somewhat intermediate between those of the Eastern and Western groups. 480 (Spiggie) is slightly less than SH, Schiehallion, but the four Shetland samples lie together apart from SH and ID, Inchnadamph, which has an unusually low value for the Western group.

(2) *Internode Ratio*. The values all lie at the upper end of the scale of Eastern plants, only 482 (Sumburgh) exceeding it. Even this is less than ID (Inchnadamph), although it is rather higher than that of the other three Shetland groups.

(3) *Leaf Length/Width*. The values are together at the lower end of the scale, only that of 448 (Coll) being less. 482 (Sumburgh) also exceeds the aberrant DL (Dunnet Links).

(4) *Leaf-taper Index*. The values are intermediate between the Eastern and Western groups, though rather closer to the Western group, the lower members of which they overlap.

(5) *Calyx-tooth Ratio*. Except for the low value for 482 (Sumburgh) the values are again intermediate, although still rather closer to the Western group.

Thus the Shetland plants lie in an intermediate position, with a tendency to approach more closely to the Western group. Figure 9 shows the distribution of (F) for all Shetland plants, including those from the original groups E. and W. and also the distribution of groups E. and W. after the exclusion of Shetland plants.

The mode for the Shetland plants lies at 36000-39000, with a calculated mean of 34,532. The total range of Shetland plants, with a unimodal distribution, is as great as that of the other two groups together. The calculated means of these groups, when Shetland plants are excluded, are :

Western group :	42,322
Eastern group :	23,154
thus : (Western-Shetland) :	7,790
(Shetland-Eastern) :	11,378

GEOGRAPHICAL DISTRIBUTION

If the Shetland plants are discounted, the discriminant function can be used to correlate the general form of the plants, in so far as the characters used are concerned, with their geographical distribution. In Table 8 the discriminant function (mean) is shown for all mainland plants used in the analysis and for each 10 km. interval of longitude. The Eastings of the Grid Reference are used, since the Grid is easily and accurately applicable within Great Britain. In Figure 10 the mean (F) is plotted against the Eastings of the Grid Reference. From Table 8 and Figure 10 it can be seen that a sharp break occurs between NC 5- and NC 7-, between Tongue and Bettyhill in Sutherland. Owing to the small gatherings from these localities, the exact line of demarcation is possibly not entirely reliable, but the break occurs within an area of probably not more than 10 kilometres wide. East and west of these points, although there is actually some local variation, the values of (F) fall into two clearly separated groups.

TABLE 8
Correlation of F with Eastings of Grid Reference.

<i>Eastings</i>	<i>Total F</i>	<i>N</i>	<i>Mean F</i>
NB/NG 4	1,080,238	25	43210
NB/NG 5	211,464	5	42293
NG 8	649,286	15	43286
NC 0	91,730	2	45865
NC 2	395,929	10	39593
NC 3	34,655	1	34655
NC 4	298,482	7	42640
NC 5	595,523	14	42537
NC 7	52,204	2	25602
NH 8	308,133	14	22010
NC 9	278,889	13	21453
ND 1	888,568	38	23383
ND 2	202,327	8	25291
ND 3	52,067	3	17356
ND/HY 4	114,259	5	22852
HY 7	65,403	3	21801

The 14 specimens included under NH 8, in the NC series, are those from Golspie, E. Sutherland, and morphologically should be included in the Eastern Group.

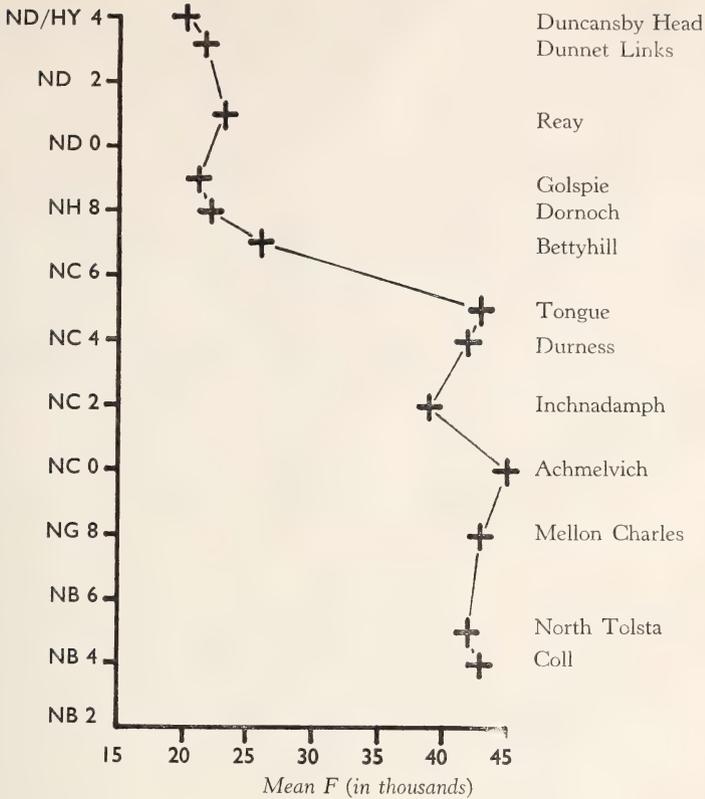


Fig. 10. Mainland and Lewis plants: correlation of F with Eastings of Grid Reference.

THE PERTSHIRE *G. SEPTENTRIONALIS*

In the foregoing discussion sample number 444 (from Tomphubil) has been included in the Eastern group of *G. septentrionalis*. It is generally similar to the plants from Caithness and Orkney, but one or two points make it worthy of further consideration. The plant was discovered by Miss M. S. Campbell in a disused lime quarry at Tomphubil, about 8 miles north of Loch Tay at the junction of the Kinloch Rannoch and Tummel Bridge roads. It has been seen since in the same place by a number of collectors including myself. There are specimens in the Oxford Herbarium, collected by Druce (1930) from Schiehallion in Perthshire, and in the Edinburgh Herbarium, collected by R. Bagnall from Blair Atholl. Both these are similar to the Tomphubil plant, and I have collected specimens from below limestone pavement at the foot of Schiehallion (? Druce's locality), about 5 miles west of the Tomphubil quarry. Subsequent investigation of herbarium material has revealed a number of other localities in Perthshire, Angus and Aberdeenshire. All these localities appear to be on small outcrops of metamorphic limestone.

The Tomphubil plants (444) differ from those from Duncansby Head (445) in a number of ways. These two populations are compared, because in both the average height of the plants is about the same (2.75 cms in 444, 1.67 cms in 445), while in 446 (Dunnet Links) it is 5.99 cm.

- Although in 444 the plants are larger, the number of internodes is rather less (2.50 to 3.08 in 445).
- Probably owing to this, the ratio internode/middle leaf is over half as large again in 444 (0.93 to 0.59; 0.94 in 446).

- (c) The contraction of the terminal internode is virtually non-existent (Internode Ratio = 1.06 in 444, 1.16 in 445).
- (d) In 444 the terminal pedicel accounts for $\frac{1}{3}$ to $\frac{1}{2}$ the height of the plant. In 445 it is less than $\frac{1}{4}$.
- (e) The Calyx-tooth Ratio in 444 is 1.30; in 445 it is only 1.11.

(a) - (d) combine to give the Tomphubil plants a rather different appearance from those of Duncansby Head, with fewer leaves, longer internodes and larger pedicels. In the samples available, there is a much more marked basal rosette in the Tomphubil plants, but this is possibly connected with a difference in duration, a notably variable feature in *Gentianella*.

In order to examine more closely the relationship between 444 and 445, a second discriminant analysis was carried out using the same characters. The resultant mean discriminant functions were found to be :

$$444 : 1781.4812$$

$$445 : 3025.8616$$

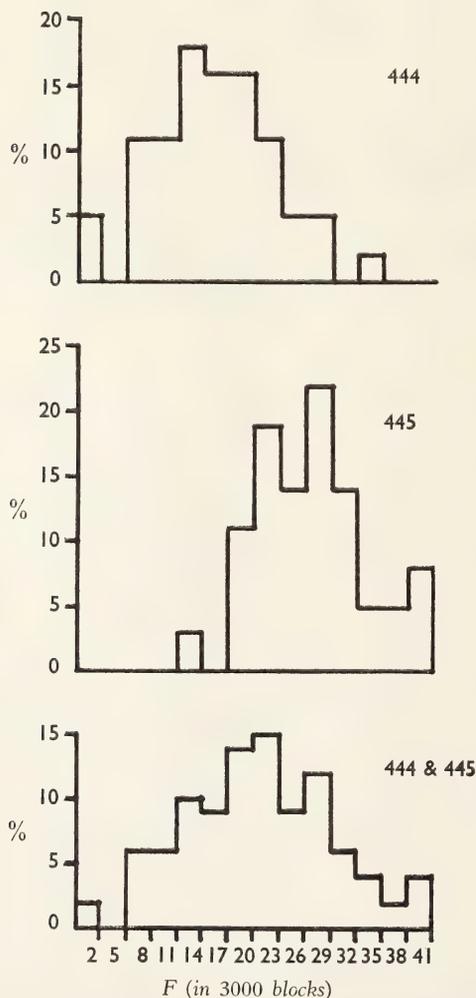


Fig. 11. Distribution of F for samples 444, 445, and 444 and 445 combined.

The discriminant function for the Perthshire plants is rather lower; this would be expected from the foregoing considerations. The distribution of (F) is shown in Figure 11, for the two groups separately and for the combined total. It is clear that the total distribution gives a close approximation to a unimodal curve, while the overlap in the separate curves includes well over half the plants. Since only two random samples were involved, the overlap might be expected to be even greater if the whole range of plants were involved.

We must conclude that, so far as the discriminant analysis involving the characters chosen is concerned, and from considering those characters separately, the distinction between the Perthshire and Caithness plants is not very significant taxonomically, though it must be borne in mind that differences of small details do exist. These differences must be considered in relation to the large disjunction in the geographical ranges of the two groups. The Perthshire plants, which grow in an inland habitat at an altitude of about 1,250ft. above sea level, about 50 miles from the nearest dunes, are 100 miles from the nearest colony of *G. septentrionalis* (at Golspie, East Sutherland). One would therefore expect some differences in morphology between them and the other populations. It seems unlikely, as no records can be traced, that *G. amarella sensu stricto* occurs between Tomphubil and the main range of *G. septentrionalis*.

Bearing in mind its general morphological similarity, including the similar flower colour, it is best to include the Perthshire plants with *G. septentrionalis* (Eastern group) despite the break in geographical distribution and ecological environment. In Sutherland (at Elphin, near Loch Eriboll, at Inchnadamph etc.) *G. septentrionalis* does occur on limestone in inland habitats, though it nowhere reaches either the distance from the sea or the altitude above it of the Perthshire plants, and the Sutherland limestone plants belong to the Western group.

TAXONOMIC CONCLUSIONS

The earliest reference to plants of the *G. amarella* agg. from Northern Scotland is that of Murbeck (1892) who gives, among other localities for *G. amarella* subsp. *axillaris*, the following: "Scotland, Caithness, Reay; Keiss Links:—W. Sutherland. Inchnadamph; Durness :—E. Ross. Coast near Tain.-Forfar.-Haddington. North Berwick." Of these, those from Forfar and North Berwick clearly refer to *G. amarella* subsp. *amarella*. The remainder, all of which must have been specimens of *G. septentrionalis*, are not distinguished by Murbeck, and it seems clear that in the absence of flower colour, to which no special reference is made, Murbeck considered all the plants he saw to represent one taxon. The chief diagnostic character of *G. septentrionalis*, the colour of the corolla (white flushed with dull red-purple outside, white or creamy within) might be included in Murbeck's "Corolla . . . sordide violacea, raro albida" or Wettstein's (1896) "Corolla violacea vel albida."

Although neither author saw any peculiarities in the Scottish plants, these had already been pointed out by Beeby (1887) some five years earlier. Beeby referred to :

"*G. amarella* L. f. *multicaulis* Lange

Unst. Abundant on the Burrafirth sands and adjacent banks below the cliffs. Differs in having the flowers brownish-red externally, and pale greenish-yellow or cream-coloured internally; corolla lobes apparently always erect, not spreading; stem usually very much branched below."

Pugsley (1936) points out that the name was not published by Lange, but only suggested

in MS. Thus Beeby's is the original valid description, and the name *f. multicaulis* Lange ex Beeby.

In 1913 Druce gave a new name to a similar plant from Ross and Sutherland.

"*Gentiana Amarella* L. nov. var. *calycina*

Planta 15–25 cm. alta est, foliis 10 mm. latis, 25 mm. longis, pallido-viridibus; corolla alba, violacea-purpurea colore tinctorum; calyx subaequalia segmenta, paulo latiora habet, quae, cum primum flores dehiscunt, plane aut fere corollae adaequant."

To this plant Druce refers Marshall's gathering no. 2440 from Tongue, and says that he has seen it also at Bettyhill (Sutherland) and Reay (Caithness).

In 1921 Druce again referred to a similar plant, this time from Shetland, in the *Flora Zetlandica*. Under the name *Gentiana Amarella* L. he says "Generally distributed on limestone and sandy pastures; Cliff and Burrafirth; Balta Island!; Tingwall!; Dunrossness!" He continues: "Forma *multicaulis* Lange. Burrafirth sands and adjacent banks!; Scousburgh, Beeby." This indicates that he himself recognized and accepted Beeby's form. He considered that the Shetland plant was sufficiently distinct from the English plant to warrant the name *Gentiana septentrionalis* nova subsp. or race (*sic*). He mentions the colour of the flowers: "Externally they are of a pale dull red, while internally the lobes are whitish, either with a trace of dull rose, or very pale grey. . . . There is no suggestion of the bluish purple of the English plant. The plants are usually more branched." When the calyx-segments are as long as the corolla, as in the plants he saw at Burrafirth and Reay, he says that the plants should be placed in the var. *calycina* of *G. septentrionalis*. This subspecies includes also the Shetland var. *multicaulis*.

In the B.E.C. Report for 1926 under "New County and other Records" there appears the following entry without diagnosis or reference:

"1763(3). *Gentiana septentrionalis* Druce.

Bettyhill, Melvich, W. Sutherland, the prevailing form, Druce."

In the Comital Flora (Druce, 1932) it is entered as a species. The entry refers to the *Flora Zetlandica* in which the plant's chief peculiarity, the colour of the flowers, is mentioned. The specific name can thus be accepted as valid. Here, the two vars. (*sic*) *calycina* and *multicaulis* are equated without comment. The first record is wrongly attributed to Druce instead of Beeby.

Because of this somewhat chequered history, the naming of the Scottish plants presents a problem. Druce's original description as a subspecies in the *Flora Zetlandica* restricts the use of the name *septentrionalis* (as subspecies and hence species) to Shetland plants from the localities listed, in which Druce himself saw the plant. In Druce's personal copy of the *Flora Zetlandica* there is a footnote in his writing; "Spiggie, Quendale, Scousburgh, Sumburgh." All these hamlets are in the parish of Dunrossness, but there is no village of that name.

The forma *multicaulis* is described by Beeby from Unst; Burrafirth sands. In the *Flora Zetlandica* this becomes a variety and "comes under *G. subsp. septentrionalis*."

The new variety *calycina* is described in Latin, and the type localities are given as Tongue and Reay. Marshall's no. 2440 is cited, and Druce's personal observations from Bettyhill and Reay.

In the first citation of *G. septentrionalis* as a species (Druce, 1926) the localities given are Bettyhill and Melvich.

PLATE 15.



E24

E24 : subsp. *druceana* (coastal race); Dunnet Links, Caithness (Holotype).

PLATE 16.



L42

L42 : subsp. *septentrionalis*;
Spiggie, Shetland (Lectotype).



T59

T59 : subsp. *druceana* (inland race);
Tomphubil, Perthshire.

The biometric work reveals the existence of two discrete groups within the species. These show small but definite morphological differences and are geographically separate from one another. For these reasons it is proposed to give them subspecific rank. The differences between *G. amarella* and *G. septentrionalis* are scarcely greater than those between the two subspecies of *G. septentrionalis*. They are principally flower-colour and -shape and again geographical separation. For this reason the two new subspecies are placed under *G. amarella*.

Druce indicated no type specimens for *G. septentrionalis*, *G. amarella* subsp. *septentrionalis* or *G. amarella* subsp. *septentrionalis* var. *calycina* in his herbarium. The following interesting specimens have however been seen. (The reference numbers are my own).

L60. Tongue, W. Sutherland. Collected 1900 by E. S. Marshall (his No. 2440). There is also a sheet of this gathering in Marshall's Herbarium at Cambridge. Labelled *G. Amarella* L. var.

L36/37. Tongue, W. Sutherland. Collected 190(?) by Druce. Labelled *G. Amarella* var. *calycina*.

E63/63b. Reay, Caithness. Collected 1902 and 1919 by Druce. Labelled *G. Amarella* var. *calycina*. (Same sheet as L36/37).

L40-44. Sumburgh, Shetland. Collected 1920 by Druce. Labelled *G. septentrionalis* Druce; also on the label is a reference to Druce (1921) and the legends: *G. Amarella* f. *multicaulis* Lange p.p. and *G. Amarella* var. *calycina* Druce p.p. (These legends are typed, and probably added later by Chapple.)

Z116/117. Spiggie, Shetland; (in Herb. Manch.) Collected 1921 by Druce, and labelled (in Druce's handwriting) *G. Amarella* L. subsp. *septentrionalis* Druce, again with a reference to Druce (1921).

The type of var. *calycina* must clearly come from either Tongue or Reay (Druce 1913). This limits the choice of a lectotype to nos. L36/37 (Tongue) or E63 (Reay). (E63a/63b, on the same sheet, are dated Reay, 1919). These two samples will be placed in different subspecies, those from Tongue in the Western one and that from Reay in the Eastern. In Druce's description of the variety, the following points (among others) are mentioned :

Plant 15 – 25 cms. high, lvs. 25 mm. by 10 mm., calyx segments subequal, equalling the corolla when the first flowers open.

These three points fit the Tongue plants very much better than the Reay plants, i.e. they fit my Western group. Of the two, L36 is chosen as lectotype since the flowers of L37 are not yet fully open.

The type of *G. amarella* subsp. *septentrionalis* must be chosen from nos. L40 – 44 or Z116 – 117, since both these were collected from the parish of Dunrossness prior to Druce's report in 1921. Both gatherings fit the description equally well, and accordingly L42 (Plate 16) is chosen as lectotype, since it is one of the most characteristic specimens, and in order that the type of the subspecies may be in Druce's Herbarium in Oxford. All Shetland plants fall into the Western group, and thus this type also is in that group.

In the first record of the name *G. septentrionalis* as a specific name (Druce 1926) the localities given are Bettyhill and Melvich, W. Sutherland. These plants fall in the Western group.

Thus all specimens that can be regarded as types for Druce's names fall within the Western group, and this becomes :

***Gentianella amarella* (L.) Börner subsp. *septentrionalis* (Druce) comb. nov.**

Gentiana Amarella f. *multicaulis* Lange ex Beeby (1887); *Gentiana Amarella* var. *calycina* Druce (1913) *pro parte*; *Gentiana Amarella* subsp. *septentrionalis* Druce (1921); *Gentiana septentrionalis* (Druce) Druce (1926); *Gentianella septentrionalis* (Druce) E. F. Warb. (1952).

Differs from subsp. *amarella* thus :

Plant 10 – 30 cm. high, of (4 –) 6 – 7 internodes. Middle and upper stem leaves ovate (to ovate-lanceolate), acute, sharply tapering with \pm widened base. Corolla (1.2 –) 1.4 – 1.6 cm. long, equalling or slightly exceeding the calyx. Calyx-teeth markedly unequal in almost all specimens. Corolla creamy white within, suffused dark purplish-red on the outside. Corolla-teeth more erect than in subsp. *amarella*.

(Because of the lack of adequate descriptions of this plant in the literature, and for the purpose of comparison with the next subspecies a description in Latin is added).

Planta 10 – 30 cm. alta, a (4 –) 6 – 7 internodiis constructa. Internodium summum breve, saepe 1 mm. longum. Folia media et superiora ovata (vel ovato-lanceolata), acuta, basim versus sat latiora quam in parte media. Corolla (1.2 –) 1.4 – 1.6 cm. longa, lacinas calycis aequans vel paullum superans. Lacinae calycis valde inaequales in plantis plurimis. Corolla intus flavo-alba, extrinsecus colore purpureo-rubro saturo suffusa. Lacinae corollae quam in subsp. *amarella* erectiores.

The biometric investigations reveal no reason for supposing that either the f. *multicaulis* of Beeby or the var. *calycina* of Druce are anything but local variations (possibly due, for example, to the high winds of Shetland) and they are accordingly not here retained as terms of any taxonomic significance.

Distribution : Shell-sand dune slacks and inland limestone from Lewis and West Ross to West Sutherland; Shetland. Because of the slight morphological differences and the discontinuity of distribution, it seems best to divide this subsp. into 2 races (cf. subsp. *amarella* (Pritchard, 1959)). These are :

- (I) Mainland and Lewis Race; Lewis, W. Ross and W. Sutherland (v.c. 105, 108, 110).
- (II) Shetland Race; Shetland, (v.c. 112).

The Eastern subspecies is given the following name, which is commemorative of Druce :

***Gentianella amarella* (L.) Börner subsp. *druceana* subsp. nov.**

G. amarella var. *calycina* Druce (1913) *pro parte exclud. typus*.

This differs from subsp. *amarella* and *septentrionalis* thus :

Plant 4 – 30 cm. high, of 2 – 5 (– 6) internodes. Middle and upper stem leaves ovate-lanceolate to lanceolate (to linear-lanceolate), not markedly expanded at the base. Terminal internode not contracted. Terminal pedicel rather longer than the internodes. Corolla (1.3 –) 1.5 – 1.7 cm. long, about $1\frac{1}{2}$ times as long as the calyx-teeth. Calyx-teeth equal or subequal, rarely unequal. Corolla colour and shape as in subsp. *septentrionalis*.

Planta 4 – 30 cm. alta, a 2 – 5 (– 6) internodiis constructa. Internodium summum non contractum. Pedicellus floris terminalis internodia aliquantum superans. Folia media et superiora (lineari-lanceolata vel) lanceolata vel ovato-lanceolata, acuta vel acutiuscula. Corolla (1.3 –) 1.5 – 1.7 cm. longa, quam lacinae calycis circa $1\frac{1}{2}$ -plo longior. Calycis lacinae aequales vel subaequales, rarius inaequales. Corolla intus flavo-alba, extrinsecus colore purpureo-rubro saturo suffusa. Lacinae corollae quam in subsp. *amarella* erectiores.

Holotypus in Herb. Oxon. Dunnet Links, Caithness. Coll. N. M. Pritchard, 19th Aug., 1955. (Ref. No. E24 of sample 446). (Plate 15.)

Distribution : Shell-sand dune-slacks and inland metamorphic limestone from Perth and Forfar to Caithness and Orkney. The marked morphological differences between plants of the two habitats suggest separation into two distinct races as a provisional measure. The differences are rather greater than those between the races of subsp. *amarella*, and forming as they do two separate geographical groups it may be desirable after further examination to divide the subspecies taxonomically.

These races are :

(1) Northern Scottish Coastal Race : North Aberdeen, Banff, E. Ross, E. Sutherland, Caithness and Orkney. (v.c. 93, 94, 106, 107, 109, 111).

(II) Inland Metamorphic Limestone Race : Perth, Forfar and S. Aberdeen. (v.c. 88 - 90, 92).

The inland plants of *G. amarella* subsp. *druceana* have usually been regarded as a form of *G. amarella* (subsp. *amarella*). Druce (1930) recorded *G. septentrionalis* from near Schiehallion, and there is a sheet of this gathering in Herb. Oxon. Nevertheless, he made no record for this species in the *Comital Flora* (1932) and from his records for *G. amarella* it is clear that he was by no means sure of the distributions of these two species.

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THE RASPBERRY WILD IN BRITAIN

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ABSTRACT

Progenies of seed of raspberry (*Rubus idaeus* L.) harvested wild from 15 English, 7 Scottish, 4 Welsh, 2 German and 2 Swiss sources were studied in the field. No new genes were found. All seedlings examined were diploid ($2n = 14$), but one rosette plant failing to flower had diploid and tetraploid shoots. The frequencies of spine colour, habit, leaf colour and leaflet number varied; one family segregated spineless plants. Most plants were hairy, in contrast to earlier reports. Investigations were made on flower bud development and flowering times; five families segregated for autumn flowering. Analyses were also made on dieback, vegetative bud-break, flower bud development, annual variation in flowering-time and fruit ripening. These biometrical characters are not essentially related to geographical origin. Male plants with healthy pollen occurred in 3 families. Males are possibly more sensitive to environment than hermaphrodites; a cycle is given to illustrate how male plants are maintained in natural populations. Six families segregated non-red fruits. Ripe fruits are mostly deep purplish-red, and markedly smaller than those of cultivated varieties. Some families had large, good flavoured fruits, suggesting derivation or introgression from cultivated varieties. The frequencies with which 7 genes were segregating in the families show a Poisson distribution. Wild raspberries are remarkably homozygous, the maximum number of heterozygous genes found in a family being four. The differences between wild and cultivated raspberries are considered in relation to the origin of "Lloyd George": wild plants usually produce many short, hairy canes, whereas cultivated varieties mostly have tall, few, subglabrous canes. The spineless character should be of use in raspberry breeding. The absence of a recognisable cline in wild British *R. idaeus* may be attributable to Great Britain representing only a relatively small area of the natural distribution.

INTRODUCTION

Although wild *Rubus idaeus* L. is described in British Floras, populations of the raspberry wild in Britain have not been studied. Bentham and Hooker (1892) stated that although generally distributed over Britain, in some localities it may have escaped from cultivation. Druce (1932) noted its occurrence throughout Britain, except for Pembrokeshire, West Cornwall and West Kent. The wild distribution can be gauged from Figure 1, which shows that it is distributed throughout Great Britain, except for the Fen areas; in Ireland its frequency decreases from the north-east to the south-west. Raspberry seeds occur regularly in inter-glacial deposits (Godwin, 1956), and it is no doubt native, at least from late-glacial time, more especially in Scotland. Raspberry seeds, in contrast to those of the blackberry, are absent from Roman deposits.

It was hoped that a study of the progenies from seeds harvested in the wild would reveal the origins of cultivated forms, and indicate whether genes from the wild could suitably be utilised by plant breeders.

MATERIAL AND METHODS

Seeds were obtained from 26 individual plants growing naturally in England, Scotland and Wales. There were also two families from Schaffhausen, Switzerland and two from the Uppener Pass, Hanover. Table 1 gives details of the source and natural habitat of the seed parents. The seeds were sown in John Innes compost and stratified during the winter of 1954-55.

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DISTRIBUTION OF "WILD" RASPBERRY (*R. IDAEUS*)
IN BRITAIN

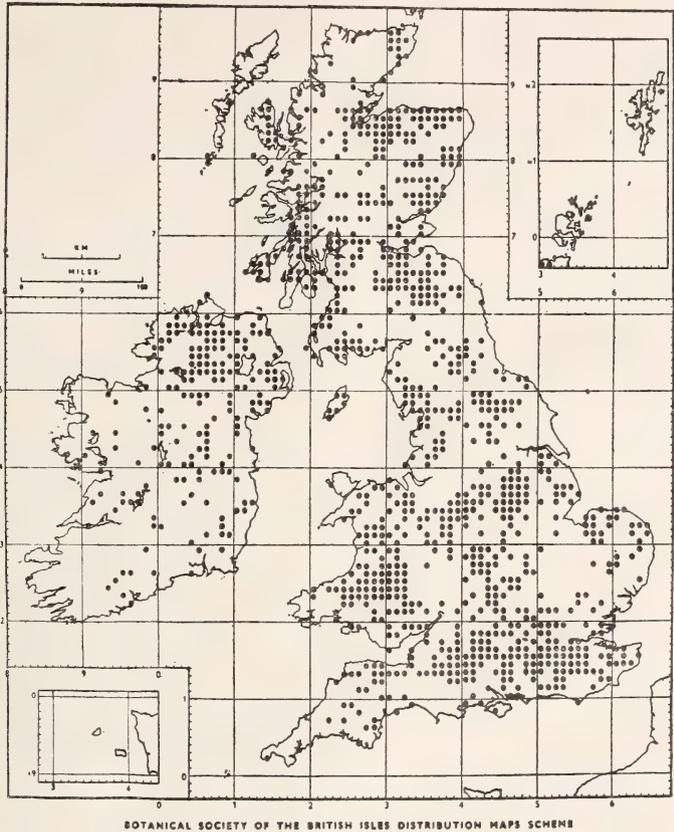


Fig. 1. Distribution map of the wild raspberry in Britain, based on records of the Distribution Maps Scheme of the Botanical Society of the British Isles. These records are not necessarily complete.

After scoring the seedlings for spine colour and intensity, and taking chromosome counts, 50 seedlings of each family were field planted in rows in June, 1955. The plants suffered badly from leather-jacket damage: the attack was at random and there was no difference between varieties in susceptibility. At an early stage the strains showed considerable variation in vigour and habit.

Several morphological characters were simply segregating, though no new morphological character simply inherited could be added to those already known in raspberry (Crane & Lawrence, 1931; Lewis, 1938, 1940); but there was confirmation for Lewis' (1941) belief that autumn flowering is genetically controlled. Biometrical measurements, for assessing differences in the strains, were taken during 1956 and 1957.

CYTOLOGY

Chromosome counts were made using Feulgen technique with 30 min. hydrolysis. Two or three young plants from each family were taken at random for examination. All seedlings were diploid ($2n = 14$).

One rosette type of plant was found with some atypical leaves in Fam. 30 from upper Teesdale, Yorkshire. Single crowns were separated from the rosette, and after further

TABLE 1
Sources of seed of wild Raspberries

Family No.	Origin	Vice-county No.	Remarks
1	East Walton Common, West Norfolk	28	Chalk. Fairly isolated
2	East Winch Common, West Norfolk	28	Peat on glacial gravel
3	Dersingham Common, West Norfolk	28	Greensand
4	Whippendell Wood, Watford, Herts.	20	
5	Yearsley Moor, Yorks.	62	ca. 500 ft.
6	Edge Hill, Warwicks.	38	Woodland
7	Annesley, Newark, Notts.	56	Permian limestone. Woodland
8	Coombe Hill, Wendover, Bucks.	24	
9	Great Ayton, Yorks.	62	
10	Caltan and Topcliffe, Yorks.	62	Yellow fruited parent in same locality for 40 years
11	Dalton Whin, Yorks.	62	
12	Kirkhill district, Easternness (Inverness)	96	Hillside. Clone of medium height
13	Kirkhill district, Easternness (Inverness)	96	$\frac{1}{4}$ mile from Fam. 12. Plant of medium height
14	Cullen, Banff	94	Roadside. Clone of medium height
15	Cullen, Banff	94	Wood about 1 mile from Fam. 14. Dwarf clone Plenty of fruit of good flavour
16	Cullen, Banff	94	Wood. Tall plant, near Fam. 15. Good flavour
17	Cullen, Banff	94	Moor 1 mile from Fams. 14, 15 and 16. Plant dwarf
18	Glenfinnan, Westernness (Inverness)	97	Moor. Plant medium height Good flavour
(19)	Schaffhausen, Switzerland	—	
(20)	Schaffhausen, Switzerland	—	
21	Nr. Mallwyd, Merioneth	48	Roadside
22	Nr. Dolgelley, Merioneth	48	
23	Nr. Dolgelley, Merioneth	48	
24	Nr. Dolgelley, Merioneth	48	Streamside
25	Springpark Wood, nr. West Wickham, Kent	16	
26	East Tisted, Hants.	11	Edge of wood
(27)	Holzberg, Stadloldendorf, Prov. of Hanover, Germany	—	Felled forest
(28)	Uppener Pass, Hildesheim, Prov. of Hanover, Germany	—	Felled forest
29	Bishopstone Downs, Wilts.	7	Clay with flints over chalk. Scrubland on summit of downs
30	White Force, Cronkley Fell, Upper Teesdale, Yorks.	65	

growth it was seen that they fell into two classes according to leaf shape. Shoots with the more rounded and darker green leaves had tetraploid roots ($2n = 28$); those with the paler green and narrower, more pointed leaves were diploid, though such leaves occasionally occurred on the tetraploid shoots. Leaves of the tetraploid crowns had a mean stomatal size of $33.0 \times 23.5 \mu$, and those of diploid crowns $21.5 \times 15.0 \mu$. The clones were subjected to transmitted light from a 100 watt lamp using a blue filter, and compared with diploid and triploid cultivated varieties of raspberries. No visible differences between plants differing in chromosome number could be detected, in contrast to those Hull & Britton (1956) found in colchicine-induced internal polyploidy in *Rubus*.

GERMINATION AND SEEDLING CHARACTERS

The germination of seeds, sown while still in the dried fruits, was generally good. The poorest germination was in Family 10 with 25%, the highest being in Family 22 with 90%. As fruits were harvested the same year the seeds were sown, wild raspberries have a good first year germination. The mean germination for 17 families was 59% (Table 2).

Three types of seedling abnormalities were observed (Table 2). Albinos occurred in six families, pleiocotyloous seedlings in eight families, and those with the first few leaves variegated in nine families. These characteristics had for all families an average frequency of .55%, .45% and 1.05% respectively. Family 11 produced nine albinos and nine variegated seedlings, suggesting a relationship between these two characters.

Family 5, from Yearsley Moor, had very rapid germination and produced very uniform dark green seedlings with coloured spines; Families 11 and 12 also had early germination and large seedlings. But by contrast Family 21 had small seedlings. Family 26, from Hampshire, differed from the others as its seedlings branched early and produced

TABLE 2
Seedling abnormalities and germination in British wild Raspberries

Family No.	No. sown	No. germinated	No. albinos	No. pleiocots	No. variegated	% germination 1st year
1	193	69	0	0	0	35.8
2	111	57	1	0	0	51.4
3	127	46	0	0	0	36.2
4	275	145	0	0	0	52.7
5	200	166	0	0	0	83.0
6	176	49	0	0	1	27.8
7	200	112	0	0	0	56.0
8	204	141	0	2	0	69.1
9	208	165	0	1	0	79.3
10	216	54	2	0	4	25.0*
11	218	154	9	0	18	70.6
12	220	118	6	0	9	53.6
13	—	203	0	3	0	—
14	230	154	0	0	0	67.0
15	—	116	0	1	0	—
16	240	187	0	0	0	77.9
17	—	306	0	0	0	—
18	—	166	0	0	1	—
19	—	47	0	1	0	—
20	—	243	3	0	1	—
21	—	61	0	0	0	—
22	280	251	0	4	0	89.6
23	240	156	0	0	5	65.0
24	—	67	0	5	0	—
25	215	148	0	1	0	68.8
26	—	182	0	0	0	—
27	—	135	0	0	0	—
28	—	154	1	0	1	—
29	—	154	0	0	2	—
Total seedlings 4,006			% of total seedlings			Mean 59.3
			0.55	0.45	1.05	

*Very weak; all light green, yellow fruited.

leaves on short internodes. The vigour was uniform in most of the families, but the seedlings were very irregular in Family 19 from Switzerland. In Family 23 there was a yellowing of the second leaves in seven seedlings out of 60, and this also occurred in Family 29. Family 6 had small, irregular seedlings and seven out of 30 were tiny; one had white picotee edges. Mottled seedlings occurred in three families, there being five mottled in a total of 62 seedlings.

Although the families were diploid and sexual, they were highly uniform other than for spine colour and intensity. There appears to have been natural selection for a developmental balance between seedling vigour and environment leading to uniformity in the seedling population. It would be very difficult to separate these diploid, sexual populations from seedlings of constant species-hybrids of *Rubus*, or from cryptically hybrid polyploid apomicts with a high proportion of apospory.

The spine colours of seedlings (Table 3) were scored at the 5-6 leaf stage, and four grades were given (0 = green spines; 1 = tinged; 2 = pale coloured; 3 = dark coloured). Grade 0 seedlings are probably equivalent to the genetic classes *pt* and *Pt*; grade 1 to *pT* and grades 2 and 3 to *PT*. Family 10 from Yorkshire was unique in producing all green spined seedlings: the original fruit from which these were raised was yellow.

TABLE 3
Spine colour segregation. % distribution in seedlings scored at 5-6 leaf stage on 16 May 1955

Grade Group	0 Green	coloured			Unclassified
		1 Tinged	2 Pale	3 Dark	
Fam. 1	0	22.1	34.0	35.7	10.2
2	0	25.9	50.0	20.4	3.7
3	0	19.0	23.8	57.1	0
4	1.7	47.3	40.6	10.1	0
5	1.7	33.4	35.1	30.1	0
6	13.3	43.3	16.7	13.3	13.3
7	0	10.0	60.1	30.1	0
8	1.7	43.4	51.8	3.3	0
9	0	56.8	40.1	1.7	1.7
10	97.6	0	0	0	2.4
11	0	23.1	33.8	37.4	5.3
12	20.0	38.6	24.3	14.3	2.9
13	8.5	13.5	55.8	20.3	1.7
14	3.3	36.7	50.1	10.0	0
15	6.8	20.2	40.6	30.4	1.7
16	1.7	28.8	52.5	15.3	1.7
17	20.0	16.7	43.4	18.4	1.7
18	0	11.7	45.1	43.4	0
19	6.9	17.3	48.3	6.9	20.7
20	6.7	53.4	23.4	16.7	0
21	0	46.6	37.3	7.0	9.3
22	0	40.1	58.5	1.7	0
23	0	11.7	53.6	53.6	9.3
24	25.4	37.2	23.7	8.5	5.1
25	10.3	8.6	56.8	18.9	5.2
26	0	3.3	35.1	60.1	1.7
27	10.2	55.1	26.5	6.1	2.0
28	10.0	33.4	38.4	15.0	3.3
29	0	18.4	45.1	31.7	5.0

Green-spined forms are of three kinds; but all are recessive for *T*, the colour producing factor. Of the 29 families, 12 failed to segregate any green-spined seedlings, 16 segregated coloured *v.* non-coloured, and only one family (Family 10) produced no coloured seedlings. There is a ratio of 1 green to 17.31 coloured throughout the whole population, excluding Family 10, with a mean of 3 green to 51 coloured per family.

In Family 12, where seven of the 29 seedlings were devoid of spines, the lack of anthocyanin in the leaves of three seedlings indicated grade 0, and four of the seedlings showed a probable grade 1.

HABIT

The habit of the plants within each family was fairly uniform, although there were general differences between families. There was a range from straggly to upright, and dwarf to tall plants. Family 10 was a very weak, non-anthocyanic family and originated from a site where yellow raspberries had been growing for 40 years, suggesting a history of self-pollination leading to inbreeding depression during this period. Family 14 (Nr. Cullen, Banff) was somewhat vigorous, and so was Family 15 from the same source, although believed to have originated from a dwarf plant, rather suggesting that the seed parent had been cross-pollinated by a normal plant.

An outstanding feature was the heavy cane production (Fig. 2). The plants had an average of 71 canes each in their second year of growth, with a range from 31 to 127 canes per plant. Most plants had between 70 and 80 canes. At the end of their annual growing period, the canes averaged only 52 inches tall, with a range of from 39 to 72 inches. The populations of wild strains have many short, thin canes, in contrast to standard cultivated varieties. This may be advantageous for survival under natural conditions, especially in areas where dieback is severe.

The tone of green colouration of the leaves bore some relationship to seed source. The two Swiss and the two German families were distinct in having smooth, olive-green leaves, in contrast to the less smooth and lighter green leaves of British families. Family 4 (obtained locally from Watford, Herts.) had a very fine appearance, not markedly different from cultivated types. Similarly, Family 8 (Wendover, Bucks.) and Family 9

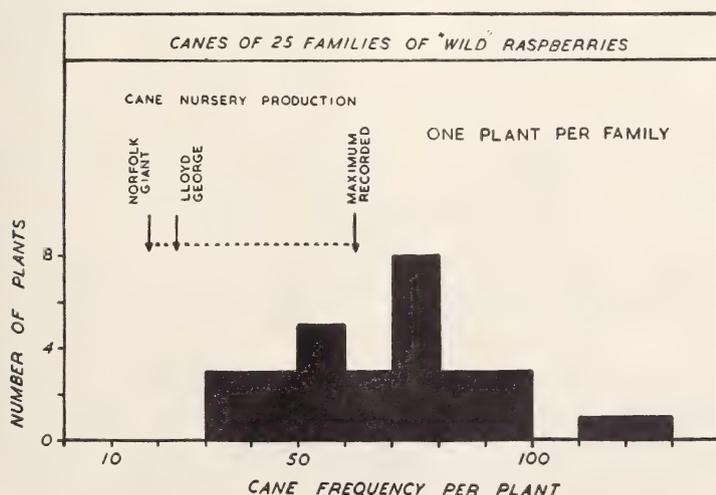


Fig. 2. Cane production in 25 British wild families. Counts are on single plants per family. The cane nursery production figures of cultivated varieties are estimates provided by Dr. C. A. Wood.

(Great Ayton, Yorkshire) had the appearance of cultivated raspberries. They had larger flowers, and fruits with a good cultivated flavour and appearance, in contrast to the smaller, darker and less pleasantly flavoured fruits of most families.

The inflorescences of the plants in Family 11 (Dalton Whin, Yorks.) lacked the deep coloration typical of the other families and of most cultivated varieties, excluding "Norfolk Giant." Their leaves were more variable than is usual for raspberries.

Leaflet-numbers on first year canes of plants within the families varied between three and five leaflets, with various intermediate grades. One family (Family 12, Inverness) was segregating plants without spines. A χ^2 test for the 40 spined to 9 spineless plants for a possible 3 : 1 ratio gave $\chi^2 = 1.14$, which is not significant ($P = 0.3 - 0.2$), and suggests it is segregating normally for this character, which results either from the parental heterozygote selfing or from sibbing with another heterozygote.

The non-prickled and prickled plants were compared in order to determine whether the lack of prickles affects vigour, as thornless wild blackberries are believed to be weaker than thorned ones. The prickled plants were 35.1 inches tall and the non-prickled were

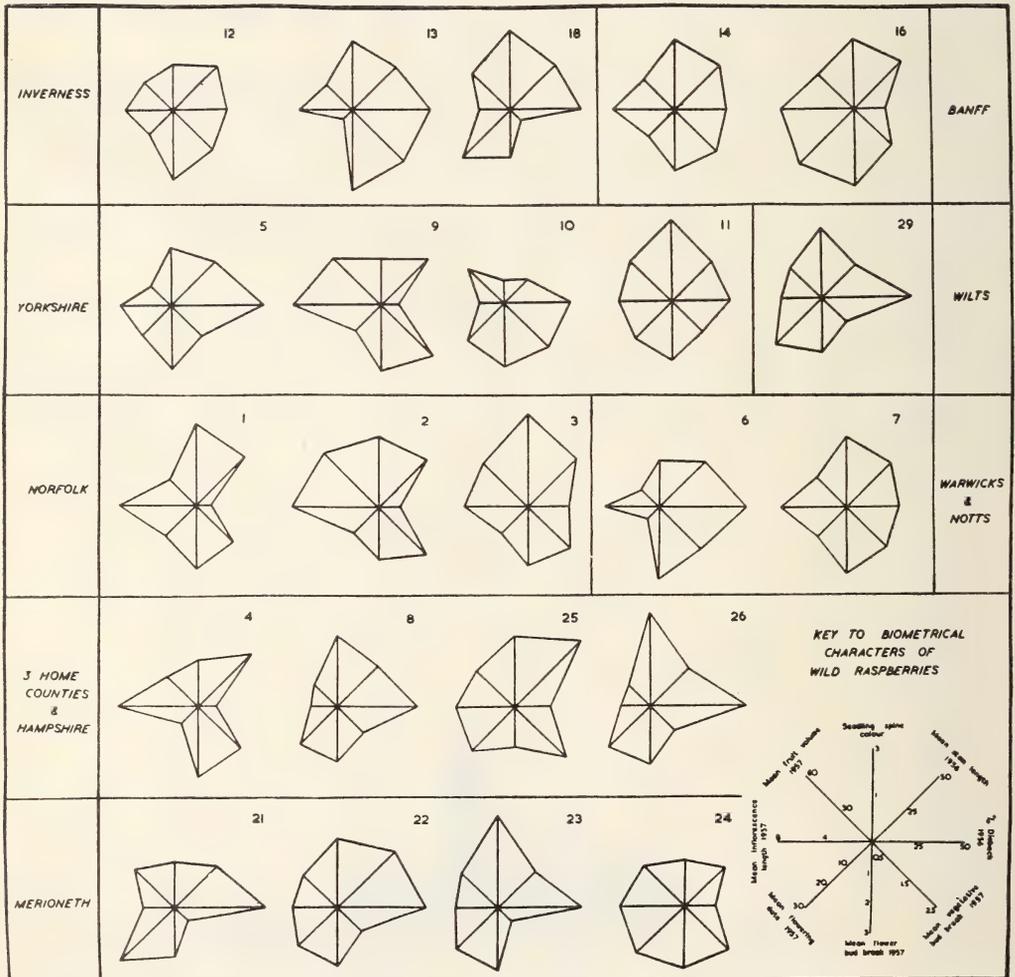


Fig. 3. Pictorial representation for eight biometrical characters in 23 British wild raspberry families, grouped according to geographical origin.

34.7 inches by 25 May, 1956; no differences in vigour are associated with the absence of prickles. The proportion of dieback in the winter of 1955-56 was 11.6% among the prickled plants, but only 4.9% among the spineless. Why these naked plants seem to over-winter with less tip-killing is not clear.

Figure 3 gives a pictorial representation of 23 of the British wild raspberry families in their mean behaviour for eight biometrical characters, with the families grouped according to their geographical origin. There is no characteristic behaviour associated with their origin, as families from the same area differ widely from each other.

HAIRY AND SUBGLABROUS STEM-TIPS

Hairiness (*H*) is most prevalent among wild raspberries (Figure 4) and only two families were subglabrous (*hh*) throughout. As classifying too early might include young plants that are first hairy but later subglabrous, scorings were made both in July and in September on two of the families (Families 1 and 13). There was a general agreement, and only four plants had to be re-classified.

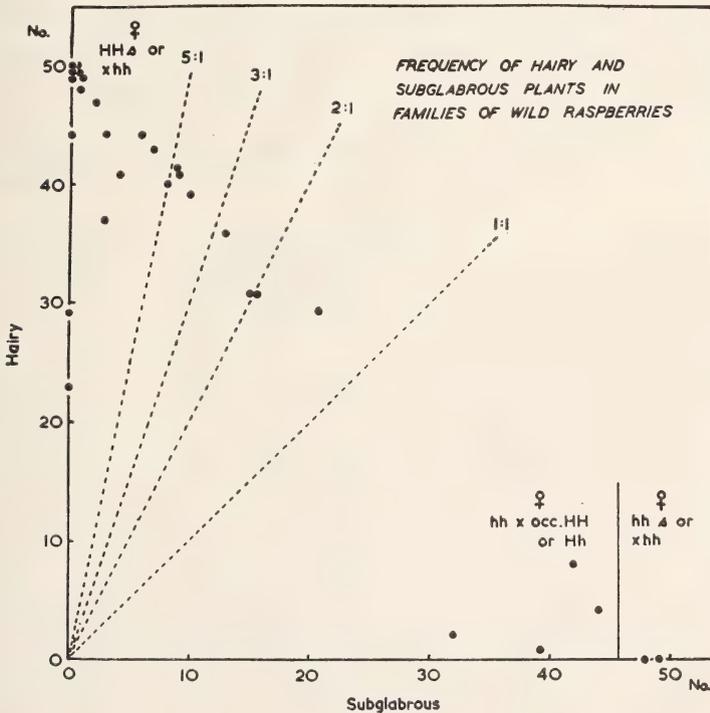


Fig. 4. Frequency of hairy plants plotted against subglabrous plants in 30 families of wild raspberries. The occasional hairy plant in an otherwise subglabrous population represents a definite cross between a subglabrous parent and a hairy pollen parent. Note the prevalence of hairy plants.

If a 3 : 1 ratio is expected from selfing or sibbing of heterozygotes (Fig. 4), then nearly all the families show a deficiency of subglabrous segregants. Grubb (1922) postulated that homozygous hairy plants do not exist in the wild; however, nine of the families were non-segregating hairy, indicating a homozygous parent. The present samplings are in contrast to the observations of Grubb who stated that in the wild the glabrous forms predominate, and that hairy plants are only found after careful search.

Four of the families were almost wholly subglabrous, with the occasional hairy plant. These must have been derived from *hh* mother plants occasionally cross-fertilised by pollen from *HH* or *Hh* plants.

FLOWERING AND POLLINATION

The developmental stages of the flowers on inflorescences were scored on 24 April, 1957 using the following key : (1) no buds showing, (2) buds clustered, (3) buds separating, (4) one flower open on an inflorescence, and (5) several flowers open. A mean statistic of flower-bud development was then calculated and the range assessed within a family, to determine whether environment has influenced this character in the history of the families. The families to show the latest flower bud development were Family 25 (West Wickham, Kent), Family 18 (Inverness), and Family 2 (West Norfolk). The earliest was Family 13 (Inverness), and this was the only family with a plant having inflorescences with several flowers open. Two other families were early : these were Family 16 (from Banff) and Family 28 (Uppener Pass, Germany).

Although the families with the earliest developing flowering buds and inflorescences were from Inverness and Banff, not all the families derived from this area are early. It is possible that a greater range of variation in this character is obtainable from this area of Scotland. This is also reflected in the mean flowering time (measured in days in June, 1956) when the families are classified by origin (Fig. 5). The Scottish families can be very early or very late. The families from the Home Counties behave likewise, but those from various parts of the Midlands, except one, are clustered together. The four families from



Fig. 5. Mean flowering time of 29 families growing at Hertford, grouped according to their geographical origin.

Wales and the four from Yorkshire are later and include no early families; they contrast especially with the Scottish families. Although there is a tendency within certain areas to produce families at one end of the flowering range, there is no definite association of this character with any geographical area.

Most families still had odd flowers and occasional buds showing on 26 June, 1957, even though ripe fruits were often present on the same plants: there is about two months extension of flowering period. No bees were seen working the raspberry plot on this date, although bees normally prefer raspberries to most other crops. The odd late flowers are less likely to be cross-pollinated than flowers at the height of the flowering season.

All the families were immensely attractive to hive bees, and various bumble bees. Although the bees are attracted by the prolific nectar, they also made regular attempts to work inflorescences that had expanded but whose buds had not yet opened (stage 3). Part of the attraction for bees may lie in the general shape of a raspberry inflorescence itself. By comparison, *Rubus caesius* L. growing on the same plot was rarely visited by bees, but attracted hover and other flies.

There were two plants with double flowers in each of Families 3 and 9. The two plants in Family 3 had extra petals, but in Family 9 one plant had double petals and sepals, and another triple sepals, and double petals from converted stamens. A gene for sepaloidy is known in raspberry; it was not possible, however, to determine whether this was the one with variable penetrance responsible for these sepaloid flowers.

AUTUMN FLOWERING

True autumn flowering is the occurrence of inflorescences terminally on the current year's canes. Confusion can be caused when there has been considerable dieback of second-year canes and new shoots arise from them low down. Autumn flowering is a discrete character and on the same plant either none of the current year's canes have terminal inflorescences or nearly all of them do. The symbols *Af-af* are assigned to it.

Five families were segregating for autumn flowering by the end of August. There was, however, no relationship between this character and the geographical origin of the families; for example, only one of the West Norfolk families was segregating for autumn flowering. Only one plant was autumn flowering in three of the families, but in Family 15 (Banff) there was a ratio of 40 summer only : 10 summer and autumn flowering, and in Family 18 (Inverness) there was a ratio of 42 : 8. χ^2 tests for each of these two families showed there were no significant differences from an expected 3 : 1 ratio.

There was no evidence, either from the appearance of the plants, or from examination of the pollen-grains of some autumn flowering plants, that they were other than diploids. This contrasts with the observations of Lewis (1941) on cultivated varieties of autumn flowering raspberries formerly grown in England, which were always either tetraploid or (occasionally) triploid.

MALE PLANTS

Male plants are readily recognised by their foliage and by the rounded shape of their flower buds. Two genes control sex: *MF* plants are hermaphrodites and *Mf* plants are males. Three families (from West Norfolk, Inverness and Merioneth) were segregating for male plants, which indicates that this gene is widely spread in the population wild in Britain. There were 106 normals and 29 males in these three families, which is very close to, and not significantly different from, a 3 : 1 ratio.

Fig. 6 shows how the male plants are perpetuated. Although they have good powers of vegetative propagation, they are unable to reproduce directly by seed; but males segregate from either selfings or sibblings of Ff plants. As male plants produce much good pollen, this will permit their crossing to FF plants, and so continue to produce hermaphrodite heterozygotes. They will give a 1 : 1 ratio of hermaphrodites and males should they backcross to the heterozygote.

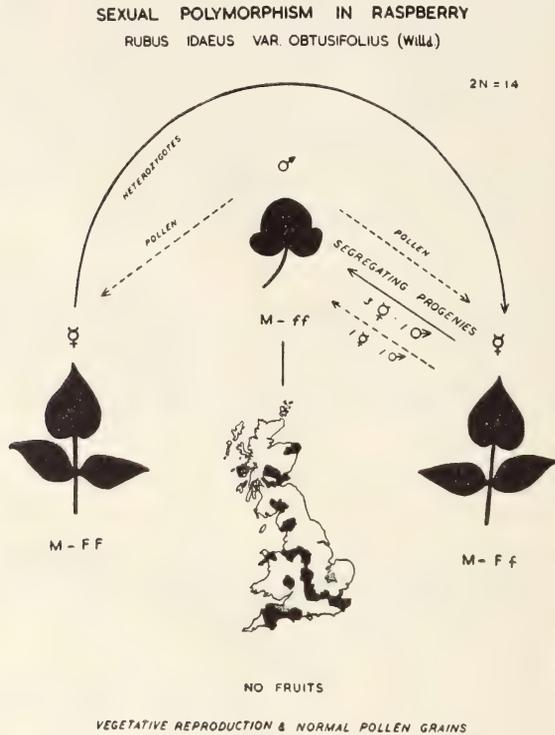


Fig. 6. The distribution of male raspberries found growing wild in Britain, and a diagram showing the pollination cycle which maintains the populations of male plants. These have fertile pollen but do not produce seeds.

Figure 6 also shows the known vice-county distribution of male plants: two doubtful records, marked in stippling, are included. Male plants have not been recorded wild in England east of the Pennines, nor until now in East Anglia. They are also absent from south-east Scotland. This suggests that plants recessive for ff are more sensitive, either during germination or in later growth stages, to the drier conditions of eastern Britain with its cold brisk winds.

The lengths and breadths of ten dry pollen grains were measured in eight wild families, six standard cultivated varieties and six inbred lines. The pollen-grains of the wild raspberries are the same size as those of cultivated varieties. There is a limited range of 7.5μ in length and of 2μ in breadth; this means that selection from the wild has not been accompanied by selection for pollen-size. Comparison in Family 3 between dry pollen-grains of hermaphrodite and male plants suggested a very slight increased size for male plants. The values for stained pollen-grains, however, were $29.8 \pm 2.2 \mu$ and $30.0 \pm 2.3 \mu$ for two hermaphrodite plants and $29.5 \pm 1.6 \mu$ and $28.5 \pm 2.4 \mu$ for two male plants; sex of the parent clearly does not influence pollen size.

FRUIT COLOUR AND SIZE

Only six families segregated for fruit colour, Table 4. Most of the red fruits were much deeper coloured, with almost a purple tone, than those of cultivated varieties, and they darkened very rapidly. In this characteristic the wild raspberries were differentiated clearly from cultivated varieties, but not all the families had "wild type" fruiting. For example, Family 2 (West Norfolk) had large, good flavoured fruits resembling those of cultivated varieties, in contrast to the small round purplish-red berries of most of the families. Such a characteristic strongly suggests that this family originated as an escape from cultivation.

TABLE 4
Fruit colour segregation. (Other families were red-fruited only)

Family No.	No. Red	No. Apricot	No. Yellow
7	13	0	2
13	25	2	0
15	31	1	0
17	34	2	0
24	44	4	3
25	41	0	1
	Total 188	9	6
10*	0	0	12
22†	50	0	0

*Yellow fruited parent.

†Amber fruited parent.

There were 188 red : 9 apricot : 6 yellow fruits in the six segregating families (Table 4). If the parents were heterozygous for *P* and *T*, the genes controlling fruit and spine colour, then the F_2 should segregate 12 red fruited : 3 apricots : 1 yellow. Even allowing for variations in the pollination system, it appears that there is an excess of red-fruited plants; Crane and Lawrence (1931) had observed that the proportion of non-red fruits in cultivated varieties was below expectation. Only one of the families was homozygous (*pptt*) for yellow fruits; on the other hand, Family 22 (Merioneth) from an amber coloured fruit produced an all-red progeny.

The distribution of fruit size in the 25 English wild families (measured as the volume of 10 fruits of ten plants in each family) and the fruit volumes of ten cultivated varieties from an adjacent plot are shown in Fig. 7. The differences in fruit size are very marked, but are unlikely to be due to differences in growing conditions, and if the cultivated clones were virus infected this would only have reduced these differences. Only the Canadian variety "Rideau" had small fruits, and there is a fair spread in size for the cultivated varieties. In the wild families, the fruits of Family 2 (West Norfolk) not only were large, but had the good flavour and general appearance of a cultivated variety. The values for size in the various wild families tended to be more clustered together. Small fruit-size is a particular character of the wild raspberry that now separates it from the modern cultivated forms.

COMPARATIVE FRUIT SIZE IN WILD RASPBERRIES

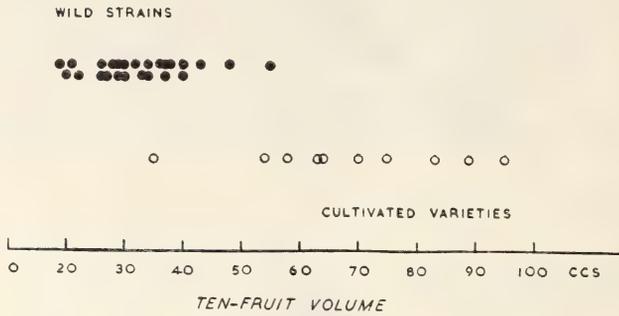


Fig. 7. Fruit sizes in the wild raspberry families compared with those of cultivated varieties growing on an adjacent plot. Fruit size is the mean volume of ten fruits for ten plants in a family, and of ten fruits in each cultivated variety.

ALLELIC FREQUENCIES

Altogether eight known genes affect habit, floral and fruit characters. They were recorded in the families (Fig. 8), but there was no segregation for green *v.* pale green leaves (*G-g*). Twelve alleles are now known in *R. idaeus* but some, such as *W-w* (which affects the pollen germination) and *X-x* (hypocotyl colour in young seedlings), require special conditions for determination. The frequencies with which the seven genes were segregating

SEGREGATIONS IN 25 BRITISH WILD RASPBERRY FAMILIES					
SYMBOL	SEGREGATING	NOT SEGREGATING		PHENOTYPE	
		DOMINANT ONLY	RECESSIVE ONLY	DOMINANT	RECESSIVE
A - a	5	20	0	SUMMER FLOWERING ON 2 nd YEAR CANES	DITTO + TERMINAL AUTUMN FLOWERING ON 1 st YEAR CANES
D - d	1	24	0	NORMAL FLOWERS	SEPALLOID FLOWERS
F - f	3	22	0	♂ FLOWERS (WITH 3-5 LEAFLETS)	♂ FLOWERS (WITH SINGLE LEAVES) = VAR. OBTUSIFOLIUS
G - g	0	25	0	DARK GREEN LEAVES	PALE GREEN LEAVES
H - h	17	7	1	HAIRY STEM-TIPS	SUB-GLABROUS STEM-TIPS
S - s	1	24	0	SPINED	SPINELESS
T - t	13	11	1	COLOURED SPINES	GREEN SPINES
P - p	6*	18	1	RED FRUITS - GREEN LEAVES	YELLOW FRUITS - PALER LEAVES (DUE TO LACK OF ANTHOCYANIN)
* INTERACTION OF P & T		{ 1 SEGREGATING APRICOT AND YELLOW 4 " " ONLY 1 " " YELLOW ONLY		EXTRA PETALS OCCURRED IN 3 FAMILIES	

Fig. 8. Description of the alleles for the eight known genes in raspberry affecting plant habit, and floral and fruit morphology, and the occurrence of these alleles in the British wild families.

are given in Fig. 9; this shows the relation between the number of families and the number of alleles for which they are segregating. There is a good fit between the observed frequencies and a Poisson distribution. Eight families segregated for only one gene and seven

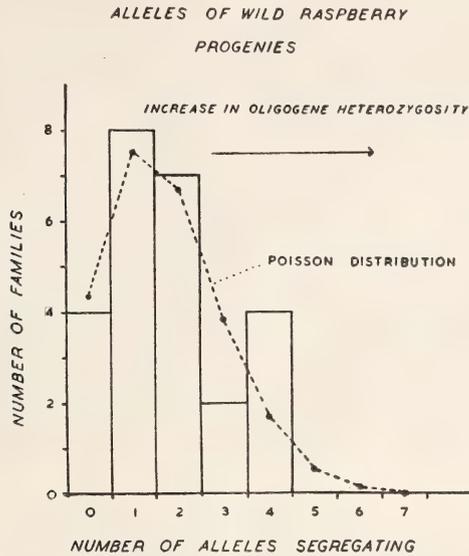


Fig. 9. The relation between the number of families and the number of alleles for which they are segregating. The theoretical Poisson distribution is also given.

for two, and it is surprising, therefore, how relatively homozygous are populations of raspberry in the wild, especially as the species is sexual and diploid. It is also curious that all five genes tested by Lewis (1938), from the 12 known, were found to be linked. The maximum number of alleles found in a heterozygous condition in any one wild family was four.

BIOMETRICAL RANGES AND CORRELATIONS

The percentage dieback to the total growth during the winter of 1956/57 showed that two families from West Norfolk, and from Hertfordshire and Yorkshire, had the least dieback, whereas three families from Hampshire, Hanover and Merioneth had the highest. Three of the four Merioneth families had over 45% dieback, yet the fourth had only 17%. Even within the same vice-county there may be wide differences in dieback, showing that being derived from a local environment is not a factor immediately responsible for the differences.

Vegetative bud-break, an important character in relation to frost damage early in the year, was measured as the mean bud-break index by 11 March, 1957. The earliest families were the two from Switzerland and Germany, whereas an Inverness family and two of the families from Merioneth were the latest. Yet another Inverness family (Family 13) was among those with the earliest vegetative bud-break in the British families; hence even this character shows no clear-cut association with origin.

In flower-bud development by April, 1957 (measured as the flower-bud index), one Inverness family was the earliest and the Kent family was the latest. The differences in mean inflorescence length on 28 April, 1957 ranged from that of a Yorkshire family (7.7 inches) to that of another Yorkshire family with inflorescences only two inches long. Thus there are considerable differences even between progenies from the same area.

The earliness of flowering, as measured by mean date in May, 1956, gave two early families: Family 13 (Inverness) and Family 16 (Banff): these were also the earliest flowering in 1957. The latest families to flower in 1956 were Family 21 (Merioneth), Family 17 (Banff) and Family 29 (Wiltshire). In 1957 only one late family was the same, *viz.* that from Wiltshire. Family 18 (Inverness) and family 24 (Merioneth) were also late. Late flowering is not so distinct and regular each year as early flowering. The contrast between early and late flowering of strains from the same area such as Inverness, together with the general annual correlation, strongly indicates that although flowering time is intrinsic to a strain, it is not necessarily related to the geographical origin.

The times taken to produce ripe fruit after flowering in 1956 were fairly close for all families. Two of the Merioneth families ripened within 34 days and 38 days respectively, whereas a Banff family and a Swiss family took 44 days. Hence even time taken to ripen is not associated necessarily with the original source. The three families with the largest fruits (as 10-fruit volume) included two of the families from West Norfolk (with 54 and 48 c.c.), and one from Yorkshire (48 c.c.). The family from Warwickshire had a mean of only 19 c.c. The largest-fruited families also had the best flavour and appearance (see Table 5), and may represent introgression from cultivated varieties, or have arisen as escapes from cultivation.

TABLE 5
The possibility of escape from cultivation or introgressive hybridisation

<i>As indicated by</i>	<i>Family No.</i>
"Cultivated" or fine appearance	4, 8, 9, 16, 25
More vigorous growth	14, 15
Largest, good flavoured fruits	2, 9
Thicker stems of inflorescences	21

Nine families out of 25 looked like escapes from cultivation.

The possibility of correlations between the means of the biometrical characters was examined. There were no correlations between mean flowering-date with percentage dieback, nor for stem-length with dieback. Mean flowering-dates in 1956 plotted against mean fruiting-dates in July showed a positive correlation, but as the mean fruiting-date range was only between 13 and 19 July, and flowering-date only from 1 to 9 June, the clustering of the time factor masked most of the correlation (*cf.* Haskell, 1955). Mean inflorescence-length on 28 April, 1957 plotted against mean flowering-time (May, 1957) shows a negative correlation, which indicates that an early assessment of the earlier flowering families might be made: but such a correlation is only to be expected, as the earlier inflorescences would start to elongate earlier.

"WILD" AND "CULTIVATED" RASPBERRIES

The absence of triploids and even tetraploids from the chromosome counts of 80 plants does not rule out their possible occurrence. The wild American red raspberry (*R. strigosus*) is diploid (Longley & Darrow, 1924), and is akin to *R. idaeus* with which it easily inter-crosses. However, three plants of *R. strigosus*, examined by Einset (1947), were triploid ($2n = 21$). Possibly these were seedlings from diploid plants in Bailey's Botanic Garden which had hybridised with cultivated tetraploid raspberries. Vaarama

(1954) examined a wild plant of *R. strigosus* from Newfoundland, which was diploid, and commented that even Longley and Darrow's observations were on cultivars derived from this species. Actually they examined one wild plant and four horticultural varieties, finding meiosis regular in all; both the wild plant and one of the varieties had 100% good pollen.

The fertility of eight British plants, determined by the frequency of well-stained pollen grains in acetocarmine jelly, gave over 75% of good grains in all plants (Table 6). There has been no selection or correlated response for increased pollen grain size and changes in fertility during domestication of raspberry from the wild. Selection in the cultivated raspberry has mainly involved reduction in number of canes and their increased growth and vigour, as well as increases in carpel-size and larger fruits. At the same time, selection has been for those plants whose fruits remain light red after ripening, by breeders rejecting the very dark and purple-red fruiting types. The dual phenomenon of numerous and short canes of the wild types strongly suggests that the supposed truly wild ancestry of a recent cultivated variety, like "Lloyd George," is open to question. This does not, of course, rule out the more likely possibility that it is an escape growing in the wild from seeds of a cultivated variety disseminated by birds. The differences in cane and fruiting characteristics of wild (W) and cultivated (C) raspberries are given in Fig. 10.

TABLE 6
Fertility in wild and cultivated raspberries

% Pollen grains stained	Number of plants		
	Wild families	Cultivated varieties	Cultivated inbred lines
41-50	0	1	0
51-60	0	0	0
61-70	0	4	1
71-80	2	4	0
81-90	1	3	1
91-100	5	12	4

According to Markham (1936) and others, "Lloyd George" was found in a wood in Dorset by J. J. Kettle, and this origin has been widely accepted. This seems unlikely, as "Lloyd George" possesses many characters superior to those of wild plants in these experiments, e.g. it averages only 24 canes per plant. A search for raspberries in Dorset around Poole failed, and this made one also suspect that "Lloyd George" did not originate in Dorset. Oldham (1946) clearly states that Kettle obtained it as a chance seedling growing in a wood in Kent, later moving to a fruit farm at Corfe Mullen, Dorset, from where he introduced the variety in c. 1919. He also raised the variety "Corfe Mullen Wonder" from "Lloyd George."

These statements accord more with the evidence from my experiments. The "cultivated" characteristics of families raised from seed parents growing wild in Greater London (e.g. at Watford, Herts. and West Wickham, Kent) indicate that they are chance escapes of local popular varieties in cultivation, probably from seed distribution by birds. Hence it is unnecessary to attribute to "Lloyd George" an immediately "wild" ancestry, as it is most likely a segregant from a popular variety already cultivated in Kent prior to 1918. Its origin may be little different from a variety like "Norfolk Giant", believed to have appeared as a chance seedling in a Norfolk garden, i.e. from an already domesticated variety.

COMPARISON BETWEEN RED FRUITED BRITISH WILD AND CULTIVATED
RASPBERRIES

CANES		FRUITS			
VIGOUR	C	VIGOROUS (IF VIRUS FREE)	SIZE	C	LARGE OR VERY LARGE
	W	WEAK TO VIGOROUS (PROBABLY VIRUS FREE)		W	VERY SMALL OR SMALL, LARGER IN SOME FAMILIES
HEIGHT		OFTEN TALL AND FEW	DRUPELETS		LARGE
		MUCH MORE NUMEROUS AND SHORTER			GENERALLY SMALL
HABIT		ERECT, RIGID OR SLIGHTLY DROOPING. REDUCED VEGETATIVE SPREAD	TEXTURE		FIRM AT MATURITY
		ERECT, RIGID PRONOUNCED VEGETATIVE SPREAD			CRUMBLING AND GENERALLY VERY SOFT WHEN RIPE
PUBESCENCE		MAINLY GLABROUS	COLOUR		MEDIUM RED, BRIGHT, NOT DARKENING
		MAINLY HAIRY			VERY DARK RED OR REDDISH-PURPLE
COLOUR		GREEN BECOMING REDDISH	FLAVOUR		GOOD OR FAIRLY GOOD
		GREEN BECOMING REDDISH-BROWN			MOSTLY POOR (INSIPID), GOOD IN SOME FAMILIES
SPINES		SMALL, INFREQUENT OR ABSENT. GENERALLY LIGHTLY PIGMENTED	PICKING QUALITY		FRUITS CONSPICUOUS, EASILY PICKED
		INTENSE, LARGE PRICKLES. MORE HEAVILY PIGMENTED			OFTEN HIDDEN BY HEAVY CANE GROWTH FAIRLY EASILY PICKED
FOLIAGE		MEDIUM GREEN SOMETIMES WITH REDDISH COLOURATION	SEASON		EARLY TO MIDSEASON
		SAME			SIMILAR
FRUITING LATERALS		MEDIUM LENGTH RATHER SHORT, WITH SMALLER FLOWERS			

Fig. 10. Comparison between red fruited British wild and cultivated raspberries. C = cultivated stocks; W = wild families.

There are 41 subglabrous and 12 pubescent modern varieties listed in Leemans & Nannenga (1958). The subglabrous character is either attractive to plant breeders, or is linked with characters that make a good commercial variety, for this frequency contrasts markedly with that in the British wild populations. Knight, Keep & Briggs (1958) have found genetic resistance to the virus-carrying aphid in the old variety "Baumforth A," which is subglabrous. Yet somatic mutations may occur for this gene, as the usually subglabrous "Malling Enterprise" occasionally produces a few pubescent canes. Crane & Lawrence (1931) found no homozygous hairy (*HH*) forms among cultivated varieties, and heterozygotes selfed or inter-crossed gave significantly greater proportions of subglabrous forms than expected. This was not found in those wild families segregating for the gene.

Two points emerge from the standpoint of the practical plant breeder. Firstly, no characters were segregating in these families not already known to geneticists; indeed the number of genes known in raspberry is small. Secondly, except for the spineless character, none of the genes appear to offer an improvement to those already in cultivated varieties, although male-sterile lines may have value in producing F_1 hybrids. Immediately a particular gene from the wild, such as spineless, is introduced into a cultivated stock, the associated biometrical characters such as vigour, fruit-size, and general habit would also affect the cross. A series of backcrosses would be necessary before the standard of the original cultivated stock was re-attained. Hence contemporary raspberry breeding is more likely to benefit from utilisation of the available cultivated varieties, as recently demonstrated by using "Baumforth A" to obtain aphid resistance.

Although the samples were taken wild throughout Britain, this area represents

only a fraction of the northern distribution of the red raspberry. Hence it is not surprising that no clines for the biometrical characters were found. Sampling over an even wider range may show more clearly a pattern in the variation, and this viewpoint is supported by the known differences between the European red raspberry (*R. idaeus*) and North American red raspberry (*R. strigosus*). These differences, which include characters like die-back, prickle density of the upper part of mature shoots, and other minor biometrical characters, have been interpreted as indicating either that *R. strigosus* is a variety of *R. idaeus*, or that they are separate species. But, as Darrow (1920) has shown, many American cultivated varieties show a mixture of characters from both. Red raspberries are fully interfertile, and the range of variation simply represents part of the variability shown by *R. idaeus* across its northern distribution.

Further study of the variation of *R. idaeus* across its range might help to show how these differences in seemingly unimportant biometrical characters are bound up with local ecological differences. It might also help us to understand the gamut of variation which is bound up with the classification of the genus *Rubus*.

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BOOK REVIEWS

Flore et végétation des Alpes. Claude Favarger, with illustrations by P. A. Robert. Vol. I. Étage alpin. 7" x 5", pp. 271 with 32 coloured plates and 35 line-drawings, 1956. Vol. II. Étage subalpin. 7" x 5", pp. 274 with 32 coloured plates and 41 line-drawings, 1958. Delachaux & Niestlé S.A., Neuchâtel and Paris. Each volume 15 Swiss francs.

These two volumes form part of a series of handbooks entitled 'Les Beautés de la Nature,' which is analogous to the British New Naturalist series, and which presents up-to-date and illustrated accounts of European plants and animals. They are written by Dr. Favarger, who is Professor of Botany at the University of Neuchâtel in Switzerland and who is well known for his studies on the cytotaxonomy of alpine plants; and they are illustrated by the artist Paul-A. Robert. The area covered is that of the Swiss Alps, and the alpine regions of France, Italy and Austria are not specifically dealt with, apart from the Jura.

The first volume deals with the alpine vegetation (i.e. the vegetation above the tree-line) and the second with the sub-alpine vegetation (i.e. the vegetation of the Coniferous forest zone). Each volume is prefaced by a discussion in which the environment and demarcation of these vegetational zones are carefully and critically examined. The species which occur are then described, not at random, but in relation to the plant communities - the associations - in which they occur; and information about taxonomy and phytogeography is skilfully interwoven with the description of the plant community and its environment. The concept of the association, as developed by the Braun-Blanquet school of phytosociologists, is utilised as a background to the discussion, but it is not obtruded, and it is always clarifying rather than confusing. An interesting series of notes is also presented about the various families of flowering plants represented in the Alpine flora; and there is a final chapter on conservation.

In this work Professor Favarger shows himself to be a first-rate field botanist, and also a writer with a lucid and elegant style. He has succeeded admirably in combining clear presentation with scientific accuracy; and he has managed to arrange his material in such a way as to interest both the amateur and the professional. He has also been fortunate in his artistic collaborator. There are many good line drawings; but the real success is scored with the coloured plates. In each of these, M. Robert has depicted three or four species growing together in their natural habitat. These plates are at the same time, clear, accurate and pleasing; and the colour rendering is extremely good. They are an admirable aid to identification; and they also give an excellent impression of the colour and beauty of alpine flowers. To anyone with some knowledge of French and a desire to learn about the flora of the Alps, these volumes can be confidently recommended.

D. H. VALENTINE

A Cytogenetic study of the Genus Geum. W. Gajewski, pp. 416. *Monographiae Botanicae* (Warsaw), 4 1957.

Although the volume of work relevant to the biosystematics (experimental taxonomy) of the European flora is by now very large, there are still remarkably few European genera of any size which can be said to be at all thoroughly investigated by modern experimental methods. Professor Gajewski's impressive study is therefore all the more welcome, for it provides detailed information on the cytogenetic relationships of the European species in particular of the genus *Geum*, a group in which some of the earliest studies of experimental species-hybridisation were made by Marsden-Jones in this country.

Geum, as defined by Gajewski, contains 56 species, of which 25 are in the type sub-genus *Geum*, well represented in Europe. This is the sub-genus to which belong the only two British species, *G. urbanum* L. and *G. rivale* L. The almost complete inter-fertility of these two species is a familiar fact to British botanists. Gajewski's work shows that this ability to hybridise is found very widely in the genus; thus apparently all species of sub-genus *Geum* can hybridise amongst themselves, and some can also hybridise with at least some species of four other sub-genera of *Geum*. Moreover, the great majority of interspecific hybrids in sub-genus *Geum* show some degree of fertility; and crosses of *G. rivale* with several other species in addition to *G. urbanum* show almost normal fertility.

Gajewski draws the following general conclusion from his experimental study of the genus: 'The conclusion to be drawn . . . is that incompatibility [i.e. sterility] barriers often depend on factors which are not distributed within a genus in a manner strictly correlated with the morphological differentiation between species.' He goes on to reject any attempt to re-draw the morphologically-based species to fit any genetic species criterion, and points out that on the Turesson terminology of eco- and coeno-species, whole groups of *Geum* species constitute single coenospecies, and some pairs of species must be considered as single ecospecies.

Such cases, where the units delimited on a genetic criterion (whatever precise criterion is chosen) will not coincide with the traditionally-demarcated taxa using morphological criteria, are of course by no means rare in flowering plants, and are responsible for the understandable reluctance of botanists in general to use the term 'species' for any genetically-defined population unit. Gajewski's terminological difficulty can be resolved by accepting the practical necessity of a set of special-purpose terms for biosystematics separate from but related to the orthodox taxonomy. The deme terminology of Gilmour and Gregor would admirably fulfil this function; *Geum rivale* and *G. urbanum* are two species constituting (in the biosystematic terminology) a single hologamödeme.

Gajewski's work is in English throughout, and provided with a valuable bibliography. The absence of any index or summary is the only adverse criticism which can reasonably be directed against this first-class modern monographic study, which must rank with the 'classic' studies of Babcock on *Crepis*, and Clausen, Keck and Hiesey on *Layia* and other American taxa. It deserves to be widely known and studied by modern taxonomists everywhere.

S. M. WALTERS

[Since writing this review, I have received from Prof. Gajewski a reprint of a short paper summarising his *Geum* work: 'Evolution in the Genus *Geum*', *Evolution*, **13**, 378, published in September, 1959. S.M.W.]

Hegi's Illustrierte Flora von Mittel-Europa, Volume III/1, Edition 2, K. H. Rechinger. Pp. 452, with 191 text figures, and 18 plates (14 in colour). Carl Hanser Verlag, Munich, 1957-1958. Price DM.98 (bound in cloth).

Hegi's magnificent *Illustrierte Flora von Mittel-Europa*, of which the first edition was completed in 1931, has become an indispensable work in every library concerned with the European flora. Its scope was planned to cover all aspects of the biology, as well as descriptions, of the flowering plants and ferns to be found over a wider area than the title suggests, and the work is graced with a wealth of illustrations. It ranks amongst the most ambitious of botanical publications and it is also one of the most useful.

Publication of the first edition extended over a period of some 25 years, and, as successive parts appeared, treatment became more elaborate. The work first planned in 6 volumes appeared in 13 - the last three having been divided, and a supplementary volume of indexes added. The standard had so improved that the early instalments of 1906 to 1912, which had been received so enthusiastically when they appeared, later seemed inadequate by comparison with the later volumes. In 1935 and 1939, the first two volumes were replaced by second editions. These increased the number of pages by about 25%, and the number of figures by over 50%, but the general treatment was not greatly modified. After the war there was a change of publisher, and preparations were commenced for new editions of Volume III in two parts instead of one, and of the first part of Volume IV (which was already divided). It is the first of this series which is now available.

Prepared by Dr. K. H. Rechinger, the new edition of Volume III, part 1, is virtually an entirely new work. The plates and some of the text figures are repeated, but the text is entirely rewritten and rearranged on an improved plan. In the old Hegi much important material was set in long paragraphs of small print in which there was no change of type. Scientific names were set in the same type as descriptions so that there was considerable difficulty in picking out the information required. In the new version all this is changed. By the use of bold type and italics as well as roman, by breaking the accounts into paragraphs dealing with separate subjects or taxa, and using a little more space, the presentation is now all that could be desired. English users with a limited knowledge of German will find it very much easier to use.

Another general change which will be welcomed is the inclusion in headings to the families, genera and species, of references to the place of publication of the names adopted, and also often of the synonyms. The whole work is thoroughly documented with citations of important literature, in which accounts in English periodicals and books are more freely cited than is usual in Continental works. Thus, for example, Buchanan-White, Moss, Meikle and Warburg are quoted in connection with *Salix*, though I do not see any reference to Linton's *Monograph*. Excellent keys are provided to each genus, though these could be rendered more time-saving by the addition of page references or species numbers. To run down a plant quickly in a key and then be forced to use the index, or turn over numerous pages, to find the description, is an unnecessary strain on the user's patience which could easily be remedied in future parts. Consideration might also be given to breaking up the longer keys into sections, so that those who already know to which part of a large genus a species belongs can avoid having to start at the beginning of the key every time.

In this new work it is not only the information about systematics, morphology, and distribution which has been brought up to date, but also the relatively new studies of cytogenetics, plant-sociology, and pollen analysis have been added. Chromosome numbers are given throughout (sometimes in neat formulae, e.g.,

Rumex acetosa : $n = 7$ (♀), $\frac{1}{2}5$ (♂), and cytological work discussed. Dr. E. Oberdorfer has assisted with the information on ecology and sociology, and Dr. M. von Rochow with pollen studies. The collaboration of many other botanists is acknowledged including Dr. A. Schreiber, who is responsible for the accounts of *Ulmaceae*, *Moraceae*, *Cannabaceae* and *Urticaceae*, and Dr. H. Meusel, who supplied distribution maps. But it is evident that the main credit for this fine work must go to Dr. Rechinger. In the first edition it took only 209 pages to cover the families which take 436 pages in the new work. In 1912 we were provided with only 90 illustrations in the text; there are now 191. The number of plates remains unchanged, and a few of them are no longer in colour, but they are printed on a more suitable and more flexible paper, which gives better impressions and enables the pages to be turned over more easily.

The work includes accounts of *Salix* and *Rumex*, of which Dr. Rechinger has long made a special study. The treatment of *Salix* covers 92 pages and is on lines which should contain few surprises for those who have kept up to date with recent literature. Particularly useful features are the figures of the leaf types, and separate keys based on leaf characters, the female and male catkins. The account of *Rumex*, which took 22 pages in the old edition, now takes 49, and is far and away the best available treatment of the species found in Europe. Much of the material has been collected together from Dr. Rechinger's earlier papers which have stood the test of time, and the result is a clear, well illustrated revision which it would be difficult to praise too highly.

English users of this book who are now accustomed to the numerous changes in nomenclature which have been introduced in our own books in recent years, will find relatively little that is unfamiliar in the names of species occurring in Britain described in this new volume of Hegi. The major adjustment which has taken place here during the last decade has to a considerable extent brought our own system into line with that of the Continent, and the advantages become apparent when it is possible to consult a book such as this without being constantly checked by unfamiliar names. It should however be noted that Dr. Rechinger gives our common Bog Myrtle as *Gale palustris* (Lam.) Chev. with reasons for separating *Gale* from the genus *Myrica* sensu stricto. Contrary to the practice now general in Britain, trivials are spelled with an initial capital where appropriate.

The weakest feature of this book from the standpoint of British botanists is the treatment of distribution in Britain. This is common to most Continental works and is largely attributable to our own failure to provide the necessary information – a shortcoming which will be remedied when the *Atlas* which the Society has in preparation appears. For example, the northern limit of *Rumex conglomeratus* is considerably exaggerated in the map on page 381, and there is no mention on page 225 of the abundant naturalisation of *Quercus cerris* in parts of Britain. The map of the distribution of *Polygonum viviparum* on page 412 is no doubt intended to show its limits, but the result is very misleading so far as Britain and France are concerned. These, however, are matters of detail and hardly affect the general distribution over the wide areas in question.

The new Hegi is an expensive work. The volume under review costs about £8 10s. in Britain. It can be obtained on a subscription basis at the rate of about 25s. per part, of which five parts made up the present book, which helps to spread the expense but does little to reduce the cost when allowance is made for binding. Even so, it is a book which every botanist who can afford it should acquire. There is no other work which gives so much information about so many aspects of plants which occur in Britain and it is excellent value for the money. No botanical library of any consequence can afford to be without it. The post-war Hegi is more than a new edition, it is essentially a new work to an improved pattern, and Dr. Rechinger has set a very high standard indeed. The replacement of further parts of the old work will be awaited with keen interest.

J. E. LOUSLEY

Handbook of the Rubi of Great Britain and Ireland. W. C. R. Watson. Pp. 274, with 50 drawings by Ruth M. Ball and A. W. Darnell. Foreword by P. D. Sell and J. E. Woodhead. Cambridge University Press, 1958. Price 63s.

All who study brambles will welcome this important book and will be grateful not only to the author, who struggled to write it when his health was failing, but also to Messrs. P. D. Sell and J. E. Woodhead for the time and care they have spent on the MS. and to the Cambridge University Press for the excellent format. It is a pleasure to read a book with such firm pages. The printing is clear and very few misprints have been noticed. On p. 6 (line 20) 'bush' should be 'brush.' The main part of the work is preceded by an Introduction of 28 pages and an Analytical Key and followed by 50 pages of drawings. The Introduction ranges briefly over many topics. The sections on environmental variations and on classification and identification are particularly important and should be read carefully by those who wish to use the book for its primary purpose.

A perfect classification of the genus *Rubus* is perhaps impossible because there are so many cross affinities between the species. The main divisions, based on the quality of the stem armature, seem clear enough,

but even so there are several species which could be assigned to more than one of the main groups with almost equal propriety. For example, *R. chaerophyllus*, which was placed with the *Silvatici* in the 'Check-List of British Vascular Plants' (*J. Ecol.*, **33**, 337-344, 1946), is here at home with the *Mucronati*. The classification adopted in this book is much the same as that of the 'Check-List' with a few name changes and a more complicated ranking system. If it is intended to reflect "the situation that exists in nature" (p. 18), it possibly succeeds, but the Analytical Key is not easy to follow.

The descriptions of the species are admirable. Watson was an acute observer in the field and the experience of many years is summarised in this part of the book. In spite of the brevity of the descriptions there is a close attention to detail. Many of the author's observations are original and picturesque, as, for example, when he says that the calyx of *R. scissus* has usually one prickle, that the petals of *R. mercicus* become patent with the sides reflexed, that the stem of *R. neomalacus* is striate with scintillating particles, that there is usually a short prickle against a very long one on a stem of *R. heterobelus* and that the calyx of *R. rufescens* has a flat base with shouldered sides. When once a bramble is known it is often quickly spotted in the field by just such individual characteristics as these. Brambles differ from one another in colour and Watson succeeds better than most of his predecessors in using colour as a guide to identification. He describes the colour of stem and foliage very well and gives a consistent and detailed account of the floral organs of nearly every species.

Those who have had the privilege of being with Watson on his walks know that when he came upon a difficult bramble he always spent a long time examining the flowers. This is reflected in his book. The petals of a bramble are often described in as much detail as the leaves. To give one example, he writes thus of *R. podophyllus*: "Petals roundish ovate, obovate-cuneate or narrow elliptic, pointed or apiculate, remote when expanded, usually faint pink to white." He was also a connoisseur of fruit. The fruit of *R. morganwensis* he tells us is "ovoid, well developed, delicious."

Another feature of the descriptions which should be noticed is the author's avoidance of unnecessary technical terms. For example, readers will look in vain for that ugly phrase "ultra-axillary part" which Rogers used so often when he was describing a flowering branch.

But descriptions alone of a critical group with so many complexities as *Rubus* are insufficient. As Sudre, the French batologist, said, "dans le genre *Rubus* les meilleures descriptions ne permettent que rarement une interprétation certaine." It is therefore a serious omission that there are no references in Watson's book to herbarium specimens. A set of exsiccatae prepared by the author himself to illustrate his species would have been of the greatest value. Failing that there are surely plants at the British Museum which could have been cited as typical. Mr. J. E. Woodhead has done much to supply this lack and has built up at the South London Botanical Institute a collection of British *Rubi* arranged according to the *Handbook* from Watson's private herbarium. But there is, of course, no reference to this in the *Handbook* and there is no guarantee that the specimens Mr. Woodhead has selected would have been chosen by Watson himself as the best to represent his species.

The need to cite authentic specimens is all the greater because Watson's views about many species changed considerably during his lifetime. The reader who tries to collate the *Rubi* of the 'Check-List' with those of the *Handbook* will soon find that even during the last years his judgment was still fluid. Some species are re-arranged, some closely related species are combined, and twelve names, viz. *poliocladus*, *spurius*, *hemistemon*, *subopacus*, *senticosus*, *piletostachys*, *splendidus*, *cordifolius*, *rhenanus*, *pygmaeus*, *vepallidus* and *semipyramidalis*, which stand as good species in the 'Check-List,' disappear altogether from the *Handbook*. It is a misfortune that the *Handbook* does not tell us what the plants which formerly went by these names should now be called.

The record of distribution by vice-counties should be read with caution. Several species are recorded for Staffordshire on the strength of specimens which I now know were incorrectly determined and several more rest on insufficient evidence. For example, the plant which Watson named *R. axillaris* and published as a first record for Britain was a single imperfect bush which bore no fruit and produced no current year shoots and which accordingly could not be found at all the following season. Perhaps even the expert batologist should respect the rule "no stem-piece, no name" (p. 18) before claiming a new British record.

The *Handbook* describes 391 species and in view of that, many people would call its author a 'splitter,' but he was in fact, at least in his later years, a 'lumper.' The quarrel between Watson and some of his older contemporaries was not that he described so many new species himself, but that he would not always accept theirs. For example, in the *Handbook* *R. cornubiensis* is equated with *R. bifrons*, an identification which Rilstone would never allow. Watson may be right. Until we can compare the Cornish plant with a good series of authentic *R. bifrons*, who can say? I think Watson was certainly right to combine *R. buttii* and the so-called eglandular form of *R. pyramidalis*, which grows at Bere Wood, under the new name *R. favonii*. When I gathered these plants I was puzzled to find any difference between them and it was a great satisfaction afterwards to discover that Watson had reached the same conclusion about them. But is *R. castrensis* really the same thing as *R. villicaulis*, is the southern *R. purbeckensis* no different from the northern *R. danicus* and is

Watson right to equate not only *R. dummoniensis* with *R. altiarcuatus* (*R. cariensis* sensu Rogers) but both of them with the Continental *R. rotundatus*?

When the student of English brambles finds a new bush which he knows has not been described in any English work, there are two alternatives to leaving it alone. He can either give it a new name or he can hunt through the descriptions of foreign brambles until he finds one which fits his bush. Watson preferred the second alternative. He did not like to multiply names nor did he like to admit defeat. There is much virtue in that attitude, but it is nevertheless fraught with danger. A description must be very good and the student must have an exceptionally acute and wary mind, if mistakes are to be avoided. It can be assumed, of course, that whenever possible Watson compared cuttings of the new bramble with authentic specimens of the species he thought it to be. But his first hand experience of the Continental flora and his acquaintance with Continental herbaria were not extensive enough to be a bulwark against error. For example, he found a distinctive bramble in two localities in Kent which he called *R. concolor*, because he thought they matched two bushes which once grew on a sunny mountain near Eupen (Belgium) more than a hundred years ago, but which have not been seen either there or anywhere else in Europe for more than eighty years. When we compare Watson's description of *R. concolor* with that of the author of the name, we notice that they are not quite the same. Watson would probably say that the differences are too slight to matter, but they open the door to suspicion.

We are grateful to the artists for fifty splendid drawings at the end of the book. Fault can be found with details here and there. For example, the petals of *R. balfourianus* should be broad and notched, the terminal leaflet of *R. sciocharis* should have a cordate base and what has happened to the petals of *R. villicaulis*, if Watson's description of them in the text is correct? But it is better to commend the general excellence. The leaf and stem prickles of *R. londinensis* are particularly good.

The *Handbook of the Rubi of Great Britain and Ireland* is regrettably Watson's last work, but it is a good thing that we should have in one volume his final judgment on the British species. It consummates the work of a lifetime. If I were asked to give my opinion of the book in a single sentence, I should say simply this: Some of the names are doubtful; most of the descriptions are excellent.

E. S. EDEES

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AMARANTHUS IN BRITAIN

By J. P. M. BRENNAN

Various species of amaranth are by no means infrequently found in Britain, but except in a few places especially favoured by climate, such as the island of Jersey, they are usually unpredictable in their occurrence and rarely persist from one year to the next. Here and there indeed in southern England a few species, especially *A. retroflexus* and *A. albus*, may become temporarily established, but their hold seems always to be precarious and easily broken. Ripe seed is often lavishly produced, but with our present climate little fear need be felt of any of them becoming noxious weeds, their frequency of occurrence here being generally due to their repeated introduction from sources overseas.

In recent years amaranths have occurred in Britain with increased frequency. To some extent at least this has been due to the greater use on the land of wool-manure, in which seeds of various species of amaranth are very common, and a number of rare and little-known species have appeared in this way. The difficulties encountered in identifying these, and the absence of any adequate revision of the genus in English, have induced me to write some account of the recorded species and to prepare a key to help in identifying them.

The generic name has been variously spelt as *Amaranthus* or *Amarantus*. Although ἀμάραντος (meaning "not withering") was used as a plant-name by classical authors, and the spelling *Amarantus* would be philologically correct, the spelling *Amaranthus* was deliberately used by Linnaeus. In spite of an apparently erroneous attempt by the International Code of Botanical Nomenclature (1952 edition, Article 82, but reversed in the 1956 edition, Article 73) to conserve the spelling *Amarantus*, the spelling *Amaranthus* is nomenclaturally correct, and must not be altered.

Many species of *Amaranthus* are remarkably similar to one another in general appearance. In the past this has led to the widespread use of certain familiar names for species to which they do not belong, and consequent confusion, both nomenclatural and taxonomic. Much of this historical confusion has now been cleared away, but the genus remains a "difficult" one taxonomically, and accurate identification is only possible if the important characters are clearly understood beforehand and carefully interpreted from specimens being actually examined. Unless the student is already familiar with some species at least, careful dissection under a lens of part of an inflorescence is always to be recommended as a preliminary to identification.

With the exception of *A. deflexus*, our species are all annuals and usually weedy in appearance. Like plants of similar habit in other families, amaranths are greatly affected phenotypically by their environment: starved or trampled plants look altogether different from those grown in rich soil. In poor conditions, a species normally nearly a metre high may flower and ripen fruit with a total height of only two or three centimetres. The key provided in this paper must not be relied on too much in dealing with famine victims, and the collector should where possible avoid them. Certain authors have laboriously classified and named these inconstant states: a recent exponent is Priszter, in whose revision of *Amaranthus* in Hungary (Priszter, 1953) many new infraspecific taxa of this sort are made, and excellent illustrations given. Work of this sort is, I consider, misguided, of limited scientific value, and serves unnecessarily to increase the complexity of an already sufficiently difficult genus.

As has already been implied, many of the most significant taxonomic characters of *Amaranthus* are to be found in the inflorescence, the individual flowers, and the fruits. Some more detailed explanation of these may be helpful.

The inflorescence is always compound, composed of basically dichasially cymose units whose ultimate branches are, however, usually monochasial. Upon the axes of these units the flowers are closely arranged, and the units themselves are usually aggregated into very dense inflorescences or partial inflorescences. The general appearance is often a congested mass in which the individual flowers are hard to discern, and whose basically cymose structure is scarcely apparent without careful separation. In general the inflorescences as a whole may be classified into two kinds, which are usually easily recognisable: a terminal panicle whose apical part at least is leafless and often spike-like, or one composed entirely of axillary cymose clusters, the total inflorescence thus appearing leafy to its apex. With the exception of abnormal plants whose normal development has been prevented by starvation, each species usually has an inflorescence of either one sort or the other, and I have employed this easily observed character at an early stage in the key to the species.

Adding to the difficulty in picking out the densely clustered flowers is the presence of bracteoles similar in colour and often in form to the perianth-segments. Each flower is subtended by two bracteoles which are, in the upper part of the inflorescence-unit, unequal in size. The arrangement is complicated by the displacement of bracteoles through adnation to the inflorescence-axes. The size and shape of the longer bracteoles in the inflorescences, and particularly their length relative to the flowers they subtend, are of great importance in distinguishing several species of *Amaranthus*.

The individual flowers are either male or female or, through reduction, sterile. Most of the species recorded in Britain are monoecious, although a group of American species, of which four have occurred in Britain, are dioecious. The monoecious species are normally protandrous. The number, size and shape of the perianth-segments, particularly of the female flowers, are among the most important taxonomic characters employed in the genus. The perianth is persistent even in fruit, and the various features of the individual segments can be easily studied at that stage. This is the more convenient since the fruit itself is often of the utmost importance in identifying the species. A normally thin pericarp encloses a single seed. The pericarp is either indehiscent or irregularly rupturing, or else regularly circumscissile,* and the fruits of each species with which we are concerned here (with the sole exception of *A. spinosus*, which is easily separated from all the others by being spinous) behave constantly in one or the other of these two ways. The surface of the pericarp may be either smooth or muricate, and this also is frequently important. The seeds themselves are generally rather uniform, smooth, black, rarely dark reddish brown, and glossy, and while their size may sometimes be significant they are otherwise of little diagnostic value, although *A. acutilobus* has a distinctively roughened testa.

There is a marked superficial resemblance between *Amaranthus* and the genus *Chenopodium* (Chenopodiaceae), and misidentifications due to this are not infrequent in herbaria. Clapham, Tutin and Warburg (1952, page 1) separate *Amaranthaceae* from *Chenopodiaceae* by the perianth being scarios in the former family and herbaceous in the latter. This character is, however, by no means always easy to assess, and to give some additional guidance here may be helpful. In *Amaranthus* the leaves are invariably entire (neglecting the sometimes crisped or undulate margin and the sometimes emarginate or bilobed apex), while in *Chenopodium* the leaves are only sometimes entire, but are more frequently toothed, sinuate or lobed. The vesicular hairs so characteristic of many species of *Chenopodium* are quite absent in *Amaranthus*, whose hairs when present are of the

*Dehiscing by a transverse slit extending all round the middle of the fruit, so that the top of the pericarp falls away like a lid.

normal slender sort. Circumscissile fruits, so common in *Amaranthus*, are unknown among the species of *Chenopodium* occurring in Britain. Finally, the normally conspicuous bracteoles subtending the flowers of *Amaranthus* are absent in *Chenopodium*.

From time to time various species of *Amaranthus* have been recorded in Britain. In the early decades of this century much British material of the genus was sent, principally due to the energy and perspicacity of Druce, to Thellung, the leading expert on the genus at that time. In particular, all the available rich adventive material from Tweedside, described by Hayward & Druce in the *Adventive Flora of Tweedside* (1919), was seen and named by Thellung. The identifications were careful and accurate, the species involved became clearly understood, and subsequent work on the genus in Britain has benefited from the good tradition so soundly laid down.

It is necessary here also to acknowledge the debt of gratitude which I, and every other student of the genus, must owe to Thellung for his most scholarly and brilliant account of the genus in Ascherson & Graebner (1914). The complicated taxonomic relationships within the genus, the bewildering ranges of variation, and the fiendishly difficult synonymy are all set out with equal competence. There are many most valuable contributions in Ascherson & Graebner's monumental work, but I believe that none will withstand the tests of time and modern research more firmly than the revision of *Amaranthus* by Thellung. In preparing the present paper I have been guided by his wisdom more often than I can remember.

The elaborate account of *Amaranthus* by Dr. P. Aellen for the second edition of Hegi's *Illustrierte Flora von Mitteleuropa* (1959) was published when most of this paper was already complete and I thus had not the benefit of its help when I should have valued it most. It is unquestionably a very valuable contribution to our knowledge of the genus, and the series of figures of fruits and perianths of so many species is a helpful feature not to be found elsewhere. In several instances, however, I have felt it necessary to differ from the nomenclature of this account, for reasons that I hope will appear sufficient.

The key in the present paper to the species of *Amaranthus* recorded in Britain makes no attempt to be "natural" but is designed solely to make an identification with the minimum of trouble. However, the order in which the species are enumerated afterwards is intended to be "natural," and is based on Thellung's account already mentioned.

Some explanation is necessary about the way the relevant literature and synonymy is cited. So thoroughly was this done by Thellung (1914) that, in pre-1914 works, I have usually restricted myself to citing the places of first publication of names and combinations, and, as far as synonyms are concerned, to mentioning only those necessary for understanding work on the genus in Britain and the nomenclature adopted.

As for the literature and names later than 1914, I have followed personal judgement. To give the full bibliography of some widely distributed species would involve citing most of the floras of the world, with no obvious advantage to be gained. I have therefore cited various works which I hope will be useful, either for their relevance to Britain, or for their descriptions or discussions, or for their illustrations. Many competent accounts are no doubt omitted, but I can only plead that enough is as good as a feast.

To the localities also similar considerations apply. It would be of doubtful use to give under each species all the sometimes very numerous British localities in which it has made a fleeting appearance. It is more useful to give an idea of the frequency or rarity with which each species may be expected to occur as an adventive, and this I have endeavoured to do, citing precise localities only for those species which have occurred with us very rarely.

On the Continent a considerable number of interspecific hybrids in *Amaranthus* have been recorded. A complete list of these is given by Priszter (1958, 126-135). So

far I have seen no hybrid amaranths from Britain, although the possibility of their occurrence should be borne in mind. The impermanence of the species here makes it unlikely that hybrids will occur frequently.

ARTIFICIAL KEY TO THE SPECIES OF *AMARANTHUS* RECORDED IN BRITAIN

- 1a. Axils of stem-leaves mostly bearing paired spines; terminal part of inflorescence spike-like; fruits dehiscent or indehiscent **6. *A. spinosus***
- 1b. Axils of leaves without spines.
- 2a. Plants dioecious; inflorescence spiciform or paniculate, with leafless terminal part; ♂ flowers with 5 perianth-segments and stamens; ♀ flowers usually without a perianth, or with 1-2 irregular rudimentary or 5 well-developed (in 24. *A. palmeri*) perianth-segments; fruits indehiscent or dehiscent; seeds 0.75-1.25 mm. in diameter, dark reddish-brown.
- 3a. Perianth-segments of ♀ flowers absent or only 1-2 and rudimentary or lanceolate; bracts 1-3 mm. long; fruits indehiscent or dehiscent; stems and leaves glabrous or almost so.
- 4a. ♀ flowers usually without a perianth, sometimes with 1-2 irregular rudimentary perianth-segments; fruits indehiscent; bracts 1-1.5 mm. long; perianth-segments of ♂ flowers subequal, with thin non-excurrent midribs. **22. *A. tuberculatus***
- 4b. ♀ flowers with 1-2 narrowly lanceolate segments, the longer about 2 mm. long; fruits circumscissile; bracts 1.5-3 mm. long; perianth-segments of ♂ flowers unequal, the outer longer than the inner, the former with conspicuously excurrent midrib **23. *A. tamariscinus***
- 3b. Perianth-segments of ♀ flowers 5, well-developed, the inner 2-3 mm. long, spatulate, obtuse to emarginate, with green sometimes slightly excurrent midrib, the outer similar, or else longer and acute with the midrib excurrent in a point; bracts 2.5-6 mm. long; fruits circumscissile; perianth-segments of ♂ flowers unequal, the longer outer ones with conspicuously excurrent midribs.
- 5a. Stem, leaves and flowers glabrous or almost so; sometimes some pubescence on the very young stems; perianth-segments of ♀ flowers unequal, the inner 2-2.5 mm. long and spatulate, the outer one 3-4 mm. long and acute; bracts 4-6 mm. long **24. *A. palmeri***
- 5b. Stem and leaves beneath ± strongly pubescent; lower surface of leaves minutely glandular; bracts and sometimes perianth minutely ± glandular-pubescent outside; perianth-segments of ♀ flowers subequal, 2-2.5 mm. long, broadly spatulate, with strong green midrib; bracts 2.5-3.5 mm. long. **25. *A. watsonii***
- 2b. Plants monoecious; ♂ flowers with 2-5 perianth-segments and stamens; ♀ flowers with a well-developed perianth of 2-5 segments; fruits various.
- 6a. Inflorescence (of normally grown plants) forming a terminal panicle, whose apical part, at least, is leafless and often spike-like; ♂ and ♀ flowers usually with 5 perianth-segments (2-3 in 15. *A. deflexus*, 16. *A. lividus* and 17. *A. viridis*).
- 7a. Inflorescence pendulous, tail-like and normally red; perianth-segments of ♀ flowers obovate or spatulate, imbricate; style-branches recurved. **1. *A. caudatus***
- 7b. Inflorescence erect or suberect, rarely somewhat drooping, red to green; perianth-segments of ♀ flowers not imbricate (except often in 19. *A. standleyanus*).
- 8a. Fruits circumscissile.
- 9a. Perianth-segments of ♀ flowers lanceolate to narrowly ovate or elliptic, normally ± acute at apex; style-branches erect; stem subglabrous to somewhat pubescent (less so than in 5. *A. retroflexus*).
- 10a. Longer bracteoles of the ♀ flowers mostly twice as long as the ♀ perianth. **2. *A. hybridus* subsp. *hybridus***
- 10b. Longer bracteoles of the ♀ flowers mostly as long as to 1½ times as long as the ♀ perianth.
- 11a. Inflorescence green **2. *A. hybridus* subsp. *incurvatus* var. *incurvatus***
- 11b. Inflorescence red **2. *A. hybridus* subsp. *incurvatus* var. *cruentus***
- 10c. Longer bracteoles of ♀ flowers shorter than the ♀ perianth **2. *A. hybridus* subsp. *celosioides***
- 9b. Perianth-segments of ♀ flowers enlarged above, ± spatulate, obtuse to truncate.

- 12a. Stems puberulous to subglabrous or glabrous; perianth-segments of ♀ flowers with green midrib excurrent at apex.
- 13a. Inflorescence with lateral branches very numerous, close, and \pm elongate (more than 1 cm. long), forming a dense thick panicle; bracteoles linear, $1\frac{1}{2}$ - $1\frac{3}{4}$ times as long as the ♂ flowers; ♀ perianth-segments about 2 mm. long, with green midrib not broadened at or above middle, otherwise scarios; dried inflorescences, at least when young, with a characteristic pale glossy brownish tinge. **4. A. quitensis**
- 13b. Inflorescence with lateral branches very short, appearing glomerate, arranged along the elongate main axes of the inflorescence, which thus as a whole appears rather lax and slender; bracteoles half as long as the ♂ flowers; ♀ perianth-segments very spatulate, about 3-4 mm. long, with a green midrib much broadened and with little branches in middle and upper part of perianth-segment; apex of ♀ perianth-segments spinulose; dried inflorescences without any brownish tinge when young. **21. A. clementii**
- 12b. Stems densely and shortly woolly-pubescent; perianth-segments of ♀ flowers with midrib disappearing below apex.
- 14a. Longer bracteoles of ♀ flowers about twice as long as the flowers.
- 15a. Stems and inflorescence pale green **5. A. retroflexus** var. **retroflexus**
- 15b. Stems, and often inflorescence also, \pm red-tinged. **5. A. retroflexus** var. **retroflexus** subvar. **rubricaulis**
- 14b. Longer bracteoles of the ♀ flowers about $1\frac{1}{3}$ - $1\frac{1}{2}$ times as long as the flowers **5. A. retroflexus** var. **delilei**
- 8b. Fruits not circumscissile.
- 16a. Longer bracteoles of the ♀ flowers about twice as long as the flowers; perianth-segments of ♀ flowers 5, oblong-lanceolate to somewhat oblanceolate, very acute, slightly unequal, shorter ones about equalling fruit, longer ones slightly exceeding it; fruit smooth or nearly so; seeds about 0.8-1.25 mm. in diameter, smooth and glossy. **3. A. bouchonii**
- 16b. Longer bracteoles of the ♀ flowers about $\frac{1}{3}$ - $\frac{2}{3}$ as long as the flowers; perianth-segments of ♀ flowers 3-5.
- 17a. Perianth-segments of ♀ flowers 3.
- 18a. Fruit shorter than or as long as the ♀ perianth, muricate. **17. A. viridis**
- 18b. Fruit $1\frac{1}{2}$ -2 times as long as the ♀ perianth, smooth or somewhat wrinkled.
- 19a. Leaves acute; stems puberulous above; fruits twice as long as ♀ perianth, inflated, smooth; seed much smaller than the cavity within the fruit, rounded-obovoid about 1.1-2 mm. long. **15. A. deflexus**
- 19b. Leaves emarginate or subtruncate; stems glabrous; fruit $1\frac{1}{2}$ times as long as the ♀ perianth; seed almost filling the cavity within the fruit, 1.1-2 mm. in diameter.
- 20a. Fruit 1.5 mm. long; perianth-segments of ♀ flowers obtuse **16. A. lividus** subsp. **polygonoides**
- 20b. Fruit 2-2.5 mm. long; perianth-segments of ♀ flowers often acute. **16. A. lividus** subsp. **lividus**
- 17b. Perianth-segments of ♀ flowers 5, unguiculate, claw erect, limb rounded and ultimately spreading. **19. A. standleyanus**
- 6b. Inflorescence composed entirely of axillary cymose clusters, the stems thus appearing leafy to apices; ♂ and ♀ flowers often with 3 perianth-segments (4-5 in *A. acutilobus*, 10. *A. blitoides*, 18. *A. crispus* and 19. *A. standleyanus*).
- 21a. Leaves conspicuously emarginate or bilobed at apex; fruit indehiscent.
- 22a. Larger bracteoles of the ♀ flowers twice as long as the flowers, with spinescent tips; perianth-segments of the ♀ flowers usually 4; fruit 1.25-1.5 mm. long, smooth; seed circular and lenticular, minutely and densely muricate-roughened; leaves obovate-cordate **8. A. acutilobus**
- 22b. Larger bracteoles of the ♀ flowers as long as the flowers; perianth-segments of the ♀ flowers 3; fruit 3.5-4 mm. long, strongly wrinkled below; seed obovoid; leaves ovate-rhombic, elliptic, or slightly obovate **14. A. macrocarpus**

- 21b. Leaves not or scarcely emarginate or bilobed at apex.
- 23a. Bracteoles twice as long as the ♀ flowers, spinescent; perianth-segments of ♀ flowers 3, not spatulate; fruit circumscissile; plant with main stem erect or ascending; leaves spatulate.
- 24a. Plant without any red pigment. **9. A. albus** subvar. **albus**
- 24b. Plant, or at least the stem, ± tinged with red. **9. A. albus** subvar. **rubicundus**
- 23b. Bracteoles half as long as to scarcely longer than the ♀ flowers (in 20. *A. mitchellii*, to about 1½ times the length of the very spatulate ♀ perianth-segments).
- 25a. Perianth-segments of ♀ flowers 3, with a slender usually colourless mucro 0.75-1.5 mm. long at apex and often bent outwards; midrib green, narrow.
- 26a. Leaves unspotted above. **7. A. thunbergii** f. **thunbergii**
- 26b. Leaves with a reddish blotch on upper side in centre. **7. A. thunbergii** f. **maculatus**
- 25b. Perianth-segments of ♀ flowers 3-5, with a mucro up to 0.5 mm. long or none (in 12. *A. dinteri* with a spinescent tip up to 0.75 mm. long but with the apical part of the segment composed almost entirely of the strong green midrib; in 20. *A. mitchellii*, with a tip of similar length to the 5 very spatulate segments).
- 27a. Fruit indehiscent; perianth-segments of ♀ flowers 5, markedly spatulate.
- 28a. Perianth-segments of ♀ flowers narrowly spatulate, erect, appressed to the fruit; leaves 0.6-1.5 cm. long, undulate-crenate on margins. **18. A. crispus**
- 28b. Perianth-segments of ♀ flowers unguiculate, claw erect, limb rounded, finally bent outwards and spreading round fruit; leaves 1.5-5 cm. long, ± flat and entire on margins.
- 29a. Midrib of ♀ perianth-segments green, single, narrow; leaves rhombic-ovate; fruits wrinkled but not longitudinally ribbed. **19. A. standleyanus**
- 29b. Midrib of ♀ perianth-segments in the broadened part of the segment much broadened and branched, forming a green patch on the segment; fruits longitudinally ribbed. **20. A. mitchellii**
- 27b. Fruit circumscissile; perianth-segments of ♀ flowers 3-5, not spatulate.
- 30a. Perianth exceeding the fruit.
- 31a. Perianth-segments of ♀ flowers 4-5, not hooked or bent outwards; seeds 1.3-1.8 mm. in diameter; plant prostrate. **10. A. blitoides**
- 31b. Perianth-segments of ♀ flowers 3; seeds 1-1.25 (-1.5) mm. in diameter.
- 32a. ♀ flowers with 3 unequal perianth-segments, 2 (sometimes 1) of which are broadly spatulate with apex entirely green and foliaceous, the third segment smaller, narrower and entirely whitish-membranous except for a trace of green midrib near apex. **11. A. capensis**
- 32b. ♀ flowers with 3 similar perianth-segments which are ovate-lanceolate, membranous at base, green and rigid-looking above (due to thickened midrib) with branching lateral nerves and white margin; apex bent outwards in a hook. **12. A. dinteri** var. **uncinatus**
- 30b. Perianth shorter than fruit; ♀ perianth-segments 3, white with green midrib, with a short apical mucro scarcely 0.25 mm. long.
- 33a. Leaves oblong or obovate- to linear-lanceolate **13. A. graecizans** ssp. **graecizans**
- 33b. Leaves elliptic to rhombic-elliptic **13. A. graecizans** ssp. **sylvestris**

1. *AMARANTHUS CAUDATUS* L. 1753, 990; Thellung, 1914, 231; Sauer, 1950, 602, fig. 5 (p. 598); Kloos, 1953, 310; Priszter, 1953, 130, t. 17, fig. 25a (p. 181); Aellen, 1959, 478, fig. 203a-e (p. 468), fig. 239 (p. 478).

[*Amaranthus cruentus* sensu McClintock (1957); *non* L.].

A. caudatus is easily recognised on account of its long tail-like inflorescences, normally of a vivid amaranth-purple.

A. caudatus is extensively cultivated in tropical and temperate regions, but its native home is uncertain. Thellung (1914, 232) suggested an origin in tropical Africa and Asia.

In Britain it is a well-known garden plant and popularly known as Love Lies Bleeding. It is found as an occasional alien on rubbish-tips, probably always of garden origin.

The specimen No. 1117.26 in the Linnaean Herbarium exactly agrees with the species as usually interpreted.

2. *AMARANTHUS HYBRIDUS* L. 1753, 990; Thellung, 1914, 234; Sauer, 1950, 608, Fig. 6, (p. 605); Kloos, 1953, 311; Priszter, 1953, 134; McClintock, 1957, 7.

subsp. *HYBRIDUS*

Amaranthus hybridus L., 1753, 990, sensu stricto.

Amaranthus hypochondriacus L., 1753, 991, as "*hypochondriacus*"; Jovet, 1940, 362; Priszter, 1953, 145, t. 17, fig. 25e (p. 181); Jovet, 1957, 97-8, fig. 23h.

Amaranthus chlorostachys Willd., 1790, 34, t. X, fig. 19; Hayward & Druce, 1919, 179, fig. 55 (p. 180); Priszter, 1953, 135, t. 17, fig. 25b (p. 181); Aellen, 1959, 480, fig. 205 (p. 469).

Amaranthus hybridus L. subsp. *hypochondriacus* (L.) Thell., 1912, 204.

Amaranthus hybridus L. var. *hypochondriacus* (L.) Robinson, 1908, 32; Covas, 1941, 336, fig. 3 C-D (p. 335).

Amaranthus hybridus L. subsp. *hypochondriacus* (L.) Thell. var. *chlorostachys* (Willd.) Thell., 1912, 205; Kloos, 1953, 314, photo 13 (p. 313).

Amaranthus hybridus L. subsp. *hypochondriacus* (L.) Thell. "*proles*" *chlorostachys* (Willd.) Thell., 1914, 236.

A. hybridus subsp. *hybridus* includes, according to Thellung's treatment (1912), two main varieties whose rank he changed in 1914 to that of "*proles*." One of these has green inflorescences, the other red (or rarely yellow). The variant with green inflorescences is typical *hybridus*, according to the specimen in the Linnaean Herbarium No. 1117.19, and corresponds also with *A. chlorostachys* Willd. The variant with red inflorescences should be called *A. hybridus* L. subsp. *hybridus* var. *erythrostachys* Moq., 1849, 259; Kloos, 1953, 314. [*A. hypochondriacus* L., 1753, 991, sensu stricto; *A. hybridus* subsp. *hypochondriacus* (L.) Thell. "*proles*" *erythrostachys* (Moq.) Thell., 1914, 241; *A. chlorostachys* Willd. var. *erythrostachys* (Moq.) Aell., 1959, 482].

A. hybridus subsp. *hybridus* var. *erythrostachys* is so far unrecorded for Britain, although it may very well occur. The var. *hybridus*, on the other hand, more familiarly known as *A. chlorostachys*, is one of our most frequently occurring amaranths, particularly common as an introduction in wool-manure, and also doubtless introduced by other means.

Within the ambit of var. *hybridus*, there are some minor variations on record for Britain: *A. hybridus* L. var. *pseudo-retroflexus* (Thell.) Thell. [*A. chlorostachys* Willd. var. *pseudo-retroflexus* Thell., 1907, 443; Hayward & Druce, 1919, 181; *A. hybridus* L. subsp. *hypochondriacus* (L.) Thell. var. *pseudo-retroflexus* (Thell.) Thell., 1914, 239; *A. hybridus* L. subsp. *hypochondriacus* (L.) Thell. var. *chlorostachys* (Willd.) Thell. subvar. *pseudo-retroflexus* (Thell.) Kloos, 1953, 314], the first, has large bracteoles usually 5 mm. or more long, and stout dense inflorescences giving the plant an aspect recalling that of *A. retroflexus* (typical var. *hybridus* having smaller bracteoles about 3-5 mm. long and more slender inflorescences). The var. *pseudo-retroflexus* is on record for Tweedside (Hayward & Druce, 1919, 181); v.c. 6, N. Somerset, Ashton Gate tip, Bristol, 16 Oct. 1934, C. I. Sandwith; also from v.c. 12, N. Hants., Itchen Abbas, 18 Sept. 1927, C. I. Sandwith; v.c. 17, Surrey, Teddington, 3 Nov. 1928, A. R. Horwood & E. Milne-Redhead; and v.c. 18., S. Essex, Hockley, Oct. 1948, comm. S. T. Jermyn in *Herb. Kew*. The second minor variant is *A. hybridus* L. var. *pseudo-retroflexus* (Thell.) Thell.

subvar. *aristulatus* Thell., 1914, 240 [*A. chlorostachys* Willd. var. *pseudo-retroflexus* Thell. subvar. *aristulatus* (Thell.) Cryer & Horrell, 1919, 306; *A. chlorostachys* Willd. var. *aristulatus* (Thell.) Hayward & Druce, 1919, 181], which is characterised by having most of the female perianth-segments bearing at their apex "a distinct awn-like point about $\frac{1}{2}$ mm. long." This variant has been recorded for Tweedside (Hayward & Druce, 1919, 181), Bradford, Yorkshire (Cryer & Horrell, 1919, 306) and v.c. 6, N. Somerset, Bristol, Bedminster, 6 Oct. 1922, C. & N. Sandwith. Neither of these variants, however, seems to me of much taxonomic significance, or to be more than a mere form of var. *hybridus*. The specimen of *A. hybridus* in the Linnaean Herbarium, No. 1117. 19, exactly agrees with *A. hybridus* L. "proles" *chlorostachys* (Willd.) Thell. var. *genuinus* Thell., as interpreted by Thellung (1914, 238); it is not *pseudo-retroflexus* or *aristulatus*.

A. hybridus subsp. *hybridus* has with us normally green stems. An unimportant colour-variation with the stems and petioles reddish, *A. hybridus* L. subsp. *hybridus* subvar. *rubricaulis* (Moq.) Thell., 1914, 238 [*A. hybridus* L. var. *rubricaulis* Moq., 1849, 259] has been found in England:—

V.c. 11, S. Hants.: Field with wool-shoddy near Fareham, 1939, R.C.L. Burges in *Herb. Brenan*; Corporation refuse-dump on N.E. side of Southampton near Bitterne Park adjacent to R. Itchen, 1953, M. Cole in *Herb. Kew*.

Amaranthus hybridus var. *hybridus* has a wide distribution in the tropical and temperate regions of the world. It is hard to separate its native and introduced localities, but its real home may well be in the New World.

In Britain *A. hybridus* var. *hybridus* is most likely to be confused with *A. retroflexus*, from which it is usually readily distinguished by the sparser pubescence, the inflorescence running out into \pm cylindrical tail-like spikes, and by the non-spathulate female perianth-segments.

subsp. **incurvatus** (Timeroy ex Gren. & Godr.) Brenan, *comb. nov.*

Amaranthus cruentus L., 1759, 1269; v. S6o, 1927, 350; Sauer, 1950, 601, fig. 5 (p. 598).

Amaranthus hybridus L., subsp. *cruentus* (L.) Thell., 1912, 205.

var. **INCURVATUS**

Amaranthus patulus Bertol., 1837, 19, t. 2; Priszter 1953, 148, t. 17, fig. 25f (p. 181); Aellen, 1959, 483, fig. 207 (p. 469).

Amaranthus incurvatus Timeroy ex Gren. & Godr., 1846, 8.

Amaranthus patulus Bertol. subsp. *incurvatus* (Timeroy ex Gren. & Godr.) Arc., 1882, 588.

Amaranthus hybridus L. subsp. *cruentus* (L.) Thell. var. *patulus* (Bertol.) Thell., 1912, 206; Kloos, 1953, 315.

Amaranthus hybridus L. subsp. *cruentus* (L.) Thell. "proles" *patulus* (Bertol.) Thell., 1914, 244.

Grenier & Godron's *Flore de France, Prospectus*, in which *Amaranthus incurvatus* was described, is an exceedingly rare work, not in the libraries of the Royal Botanic Gardens Kew, the British Museum (Natural History), or the Linnean Society of London. Thanks to Mr. P. Taylor and the kindness of the authorities of the Conservatoire et Jardin Botaniques at Geneva, a photographic copy of the relevant parts has been made available. Since this contains apparently the only description of the name *Amaranthus incurvatus*, I reproduce it here *verbatim*:—

"*Amarantus incurvatus* Timeroy.—Fleurs pentandres, en grappes denses, fasciculées; bractées ovales-sétacées, concaves, doubles du péricône à divisions oblongues-lancéolées. Grappes et rameaux arqués-infléchis surtout après la floraison. Tige dressée, sillonnée, pubescente, simple ou rameuse; feuilles longuement

pétiolées, ovales-rhomboidales, mucronulées.-Plante d'un vert foncé; à tiges, rameaux et pétioles rougeâtres. Elle se distingue de l'*A. retroflexus* L. par sa teinte, ses grappes arquées-infléchies, ses bractées plus courtes, lancéolées, et non linéaires-rétuses, par ses feuilles plus finement ponctuées en dessous.

Hab. Tigneu, village près de Lyon, en société avec l'*A. retroflexus*. ☉."

var. *CRUENTUS* Mansf., 1959, 54.

Amaranthus cruentus L., sensu stricto.

Amaranthus paniculatus L., 1763, 1406; Guiton, 1918, 50; Priszter, 1953, 155, t. 17, fig. 25i (p. 181); Aellen, 1959, 484, fig. 208 (p. 469), fig. 239 f-h (p. 478).

Amaranthus speciosus Sims, 1821, t. 2227; Arsène, 1930, 237.

Amaranthus paniculatus L. var. *cruentus* (L.) Moq., 1849, 257.

Amaranthus hybridus L. var. *paniculatus* (L.) Uline & Bray, 1894a, 145 & 1894b, 314.

Amaranthus hybridus L. subsp. *cruentus* (L.) Thell. var. *paniculatus* (L.) Thell., 1912, 205; Kloos, 1953, 315.

Amaranthus hybridus L. subsp. *cruentus* (L.) Thell. "proles" *paniculatus* (L.) Thell., 1914, 247.

The var. *cruentus* (at least as far as Britain is concerned) comprises those variants of subsp. *incurvatus* with red or purple inflorescences. The structure of the inflorescence is, however, decidedly variable. The plant has been much grown in gardens, cultivars have arisen, and a number of them have been given botanical names (see Thellung, 1914, 248-251). There is a specimen of *Amaranthus cruentus* in the Linnaean Herbarium, No. 1117. 25, which may be taken as authentic and has long, stout, flexuous, spiciform inflorescences, and agrees with *A. hybridus* L. subsp. *cruentus* (L.) Thell. "proles" *paniculatus* (L.) Thell. var. *cruentus* (L.) Moq. as interpreted by Thellung (1914, 249), of which *A. speciosus* Sims is given as a synonym. It is closely similar also to *Augustin & Sennen, Plantes d'Espagne*, 3798 (Herb. Kew.), from Spain, prov. Gerona, Figueras, Collège Hispano-Français, 13 Oct. 1919, which is likely to have been from a cultivated plant. *A. paniculatus* L., as judged from the specimen in the Linnaean Herbarium, No. 1117. 20, is very like *A. cruentus* but has densely and profusely branched inflorescences with the lateral branches rather short, slender, and arching upwards.

It is likely that var. *cruentus* is itself a taxon that has arisen in cultivation, but has thus become widely spread, and has escaped in various places.

In Britain it is a rather rare alien of rubbish-tips and waste ground, probably usually originating as a throw-out from gardens. It is possible that it may be more persistent in Jersey.

Although *A. paniculatus* L. var. *sanguineus* Regel (Mar. 1849) antedates var. *cruentus* Moq. (May 1849), the possibly typical form of the former is referred by Thellung to subsp. *hybridus*, others of its forms coming under subsp. *incurvatus*. I consider that *cruentus* should stand.

[subsp. *CELOSOIODES* (H.B.K.) Thell., 1914, 251.

Amaranthus celosioides H.B.K., 1818, 194; Sauer, 1950, 608, fig. 6 (p. 604); Aellen, 1959, 483, fig. 206 (p. 469).

This subspecies of *A. hybridus*, outstanding on account of its very short bracteoles, is native of South America, but has not yet been recorded with certainty from Britain though it may well occur].

3. *AMARANTHUS BOUCHONII* Thell., 1926, 4, as "*bouchoni*"; Jovet, 1940, 365, fig. Bo 1-4 (p. 366); d'Alleizette & Aellen, 1953, 161; Jovet, 1957, 97-8, fig. 23, Bo; Aellen, 1959, 475, fig. 200 (p. 468).

The origin of this species is unknown. It was first described from France, and has become, according to Jovet (1940), locally common especially round Paris (where I have seen it) and to the northwards, and also in south-western France round Bordeaux, Toulouse and Périgueux. It is also in Germany and Switzerland (Aellen, 1959, 475-6).

In Britain the species has been found twice, as follows :—

V.c. 25, E. Suffolk : Brantham, weed on farm, comm. Nov. 1959, *N. R. Kerr* in *Herb. Kew.* V.c. 28, W. Norfolk : arable land, Rowley Corner, Hilborough, in a crop of annual blue lupin, Sept. 1954, *E. L. Swann* 2524.

The Norfolk specimen was distributed through the Exchange Section of the B.S.B.I. wrongly determined, by myself, as *A. hybridus*, subsp. *cruentus* var. *patulus* (see Graham, 1955, 581).

Amaranthus bouchonii is strikingly similar to *A. hybridus* subsp. *hybridus* except for the indehiscence of the fruits. Tucker & Sauer (1958) have discussed certain aberrant populations of amaranths occurring in the Sacramento-San Joaquin Delta in California and involving hybrids between *A. caudatus*, *A. cruentus* (treated by them as a species), *A. hybridus*, *A. powellii* S. Wats. and *A. retroflexus*. They found that in certain plants of these complex populations the fruit often fails to dehisce, although this character is unknown in any of the five species involved. They suggest that *A. bouchonii* represents a genotype of similar hybrid origin occurring in Europe. The abundance and constancy of *A. bouchonii* on the Continent makes this suggestion not altogether convincing. An origin through mutation from *A. hybridus* seems at least an equally likely explanation.

4. *AMARANTHUS QUITENSIS* H.B.K., 1818, 194; Thellung, 1914, 252; Sauer, 1950, 608, fig. 6 (p. 604); Kloos, 1953, 315; Priszter, 1953, 159, t. 10 (p. 161) t. 17, fig. 25j (p. 181); Aellen, 1959, 487, fig. 210 (p. 470).

Amaranthus hybridus L. var. *quitensis* (H.B.K.) Covas, 1941, 336, fig. 3A-B (p. 335).

A native of South America, occurring from time to time in Britain as a rare alien near docks, on rubbish-tips, and as an introduction with wool-manure.

A. quitensis is similar both to *A. hybridus* subsp. *hybridus* and to *A. retroflexus*, but is distinguished from both by the ♀ perianth-segments and from *A. retroflexus* by the much less hairy stems. It is a late flowerer with us, seldom if ever fruiting. In the dried state the ♂ flowers have a characteristic pale brownish glistening sheen which I have not observed in the related species.

5. *AMARANTHUS RETROFLEXUS* L., 1753, 991; Thellung, 1914, 254; Hayward & Druce, 1919, 176; Sauer, 1950, 605, fig. 6 (p. 604); Clapham, Tutin & Warburg, 1952, 342; Kloos, 1953, 316; Priszter, 1953, 162, t. 16, fig. 24 b,c (p. 175), t. 17, fig. 25k (p. 181); Aellen, 1959, 485, t. 95, fig. 5, 5a, c-e, fig. 209 (p. 470), fig. 241 (p. 486), fig. 242 1-r (p. 505).

var. *RETROFLEXUS*; Aellen, 1959, 486.

Amaranthus retroflexus L. var. *genuinus* Thell., 1914, 259.

According to Thellung (1914, 255), probably of North American origin; now common in Europe also, and introduced into other parts of the world.

In Britain it is perhaps our commonest amaranth on rubbish-heaps, near docks, and also as a weed in cultivated ground, sometimes showing a tendency to persist from year to year. As an introduction with wool-manure it seems rather rare. It is normally easily identified by its paniculate terminal inflorescence, lobed but not with "tail-like" branches, by its densely pubescent stems and by its spatulate ♀ perianth-segments.

It is normally green (subvar. *retroflexus*) but a variant with a reddish tinge on the stems and inflorescences (*Amaranthus retroflexus* L. subvar. *rubricaulis* Thell, 1914, 260; *Amaranthus retroflexus* var. *rubricaulis* (Thell.) Sandwith, 1953, 414) has been once found: V.c. 18, S. Essex: Dagenham, N. Y. Sandwith 3958.

The specimen No. 1117.22 in the Linnaean Herbarium is certainly the species as usually interpreted. I think that it is almost certainly var. *retroflexus* but the specimen is immature.

var. *DELILEI* (Richter & Loret) Thell., 1907, 442; Thellung, 1914, 260; Hayward & Druce, 1919, 176; Kloos, 1953, 317; Priszter, 1953, 180, t. 17, fig. 252 (p. 181); Aellen, 1959, 486.

Amaranthus delilei Richter & Loret, 1866, 316.

The var. *delilei* has much the same general distribution as var. *retroflexus*, and is connected with it by some intermediates. In Britain it is somewhat less common than var. *retroflexus* but nevertheless not infrequent. It is separated from var. *retroflexus* only by the shorter bracteoles, as mentioned in the key (p. 265).

6. *AMARANTHUS SPINOSUS* L., 1753, 991; Thellung, 1914, 267; Kloos, 1953, 317; Aellen, 1959, 477, fig. 202 (p. 468).

A. spinosus, unique among our amaranths in producing paired axillary spines, is a pantropical species rarely seen in Britain and then usually near docks or as an introduction with wool-manure. *A. spinosus* is also remarkable in having the fruits indehiscent or irregularly dehiscent, or regularly circumscissile (? varying on the same plant).

The specimen No. 1117. 27 in the Linnaean Herbarium exactly agrees with this species as usually interpreted.

7. *AMARANTHUS THUNBERGII* Moq., 1849, 262; Hayward, 1914, 332, *cum tab.*; Thellung, 1914, 280; Hayward & Druce, 1919, 181; Kloos, 1953, 319; McClintock, 1957, 7; Aellen, 1959, 496, fig. 223 (p. 471).

A. thunbergii is indigenous in tropical and South Africa. In Britain it is one of the most frequently occurring amaranths where wool-manure has been used and is rarely introduced through any other means.

The upper surface of the leaves is normally green, but Thellung (1919, 306) described a f. *maculatus*, with the leaves bearing a reddish blotch in their centre. The type-collection was made by J. Cryer at Bradford in Yorkshire, but in recent years the same form has occurred as an occasional introduction with wool-manure in other localities in England.

8. *AMARANTHUS ACUTILOBUS* Uline & Bray, 1894, 10, 320; Thellung, 1914, 282; Sandwith, 1948, 271; Aellen, 1959, 497, fig. 224 (p. 471).

A. acutilobus is native of southern Mexico, and has with us once been recorded as a casual:—

Channel Isles: Jersey, St. Helier's, 21 Sept. 1920, *Bro. Louis-Arsène*.

The above gathering was distributed through the B.E.C. in 1929 under the erroneous name of *A. ascendens* Lois. var. *polygonoides* (Moq.) Thell. (see Sandwith, *l.c.*).

A. acutilobus is, as Sandwith has pointed out, an outstandingly distinct species, "well characterised by being quite glabrous; by the remarkably small, obcordate and deeply emarginate leaves; the small axillary clusters of flowers; the spinous-tipped outer bracts which are up to twice as long as the female flowers; the 5 tepals of the male and the 4 tepals of the female flowers; and, finally, by the ellipsoid-subglobose fruits which are smooth and indehiscent."

9. *AMARANTHUS ALBUS* L., 1759, 1268; Thellung, 1914, 283; Hayward & Druce,

1919, 179; Covas, 1941, 337, fig. 3 F-G (p. 335); Clapham, Tutin & Warburg, 1952, 342; Kloos, 1953, 320; Priszter, 1953, 180, t. 38, fig. 56a (p. 232); Aellen, 1959, 497, fig. 225 (p. 471).

A. albus is a native of North America. In Britain it is a frequent introduction on rubbish-tips, near docks, etc., and also occurs as an introduction with wool-manure. On the great rubbish-tips at Dagenham, S. Essex (v.c. 18) it occurred before the last war in immense profusion in certain places, and evidently persisted from year to year.

The specimen in the Linnaean Herbarium, No. 1117.1, exactly agrees with the species as usually interpreted.

A. albus is easily recognised by its conspicuously pale, whitish or straw-coloured, usually much branched stems; by its spatulate leaves; by its axillary inflorescences; by its spinescent bracteoles much longer than the flowers; by the flowers of both sexes having normally 3 perianth-segments; and by the circumscissile fruits.

Normally there is no trace of reddish pigment in the plant, but *A. albus* L. subvar. *rubicundus* Thell., 1914, 287 [*A. albus* L. f. *rubicundus* (Thell.) Priszter, 1953, 190], with a \pm reddish tinge, has been once found:—

V.c. 28, W. Norfolk: Appleton, carrot-field alien, 1 Oct. 1949, *C. E. Hubbard*.

10. *AMARANTHUS BLITOIDES* S. Wats. (1877) 273; Thellung, 1914, 290; Jovet, 1940, 369; Brennan & Sandwith, 1948, 269; Kloos, 1953, 320; Priszter, 1953, 191, t. 38, fig. 56c (p. 232); Aellen, 1959, 489, fig. 214 (p. 470).

A. blitoides is a native of North America, and, though first recorded for Britain as recently as 1948, has occurred rather frequently in recent years, usually on rubbish-tips and waste ground, but also occasionally as a wool-alien.

A. blitoides is closest in appearance to *A. graecizans*, from which it differs in the ♀ perianth-segments equalling or exceeding, not shorter than, the ripe fruit. It differs from *A. thunbergii* in the ♀ perianth-segments being shorter, separated from one another to base and not overlapping, with narrower, less markedly scarios margins and a shorter apical spinule.

11. *AMARANTHUS CAPENSIS* Thell., 1914, 293; Kloos, 1953, 322; Aellen, 1959, 502, fig. 232 (p. 472).

This rare and little-known species is native of South Africa. Thellung based his species on Ecklon & Zeyher 88, but no other South African material, at least at Kew, appears to have been hitherto identified with it. No Ecklon & Zeyher specimen bearing the number 88 has been traced in the herbaria at Zürich, Vienna, Paris, Kew, or Oxford, or in the Gandoger Herbarium at the Faculté des Sciences, Lyon. It is quite likely that the holotype was destroyed at Berlin, but a duplicate may well exist in some herbarium not so far searched. If one is found, the writer would be glad to know. Meanwhile the species must be interpreted from description. The following specimen, issued from the National Herbarium at Pretoria as *A. thunbergii* Moq., agrees well with Thellung's description of *A. capensis*:—

SOUTH AFRICA. Cape Province, Willowmore Division, 9 Nov. 1950, *G. C. Theron* 907 (Herb. Kew.):—prostrate on sandy soil; leaves slightly succulent.

A. capensis has been collected twice in England, as a wool-alien:—

V.c. 37, Worcs.: Evesham, Charlton, 17 Aug. 1958, *C. W. Bannister* in *Herb. Lousley*, W 780. Same locality, Sept. 1959, *C. W. Bannister*.

A. capensis is evidently related to *A. thunbergii* and *A. dinteri*, but is characterised by two (or sometimes one) of the three ♀ perianth-segments being spatulately enlarged,

green and leafy above, acute to obtuse, with a very short apical spinule scarcely 0.3 mm. long.

12. *AMARANTHUS DINTERI* Schinz, 1900, 15; Thellung, 1914, 295; Aellen, 1959, 502.

var. *UNCINATUS* Thell., 1913, 74; Hayward & Druce, 1919, 181, fig. 56 (p. 182); Kloos, 1953, 323; Aellen, 1959, 503, fig. 233 (p. 473).

Amaranthus dinteri Schinz "proles" *uncinatus* (Thell.) Thell., 1914, 296.

A. dinteri is a native of South Africa. *A. dinteri* var. *uncinatus* has occurred in several localities as a wool-alien, though it seems decidedly scarcer than *A. thunbergii*, to which it bears a considerable similarity. The conspicuously hooked, rather rigid-looking apices of the bracteoles and ♀ perianth-segments usually make *A. dinteri* var. *uncinatus* readily separable. Typical *A. dinteri* (var. *dinteri*; *A. dinteri* Schinz "proles" *typicus* Thell. (1914, 296), characterised by its bracteoles and ♀ perianth-segments with their apices straight or only slightly bent outwards, has not so far been found in Britain. Two plants, perhaps best considered as intermediates between var. *dinteri* and var. *uncinatus*, with the apices partially hooked or else less so than in normal var. *uncinatus*, have occurred as follows:

V.c. 37, Worcs.: Charlton, shoddy-field, comm. 3 Nov. 1959, C. W. Bannister.

V.c. 63, S.W. Yorks.: Linthwaite, 27 Sept. 1959, D. McClintock in *Herb. Lousley* 1117.

13. *AMARANTHUS GRAECIZANS* L., 1753, 990; Fernandes, 1957, 189-192; Aellen, 1959, 500.

subsp. *GRAECIZANS*

Amaranthus angustifolius Lam., 1783, 115, *nom. illegit.*; Hayward & Druce, 1919, 177, fig. 54 (p. 178).

Amaranthus angustifolius Lam. "proles" *graecizans* (L.) Thell., 1914, 306.

Amaranthus angustifolius Lam. var. *graecizans* (L.) Thell., 1918, 49.

Amaranthus graecizans L. var. *graecizans*; Aellen, 1959, 501.

A. graecizans subsp. *graecizans*, hitherto usually known under the illegitimate name *A. angustifolius* Lam., seems to be native of the Mediterranean region, tropical Africa, and western Asia. In Britain it is a rather rare alien of rubbish-tips and waste ground.

A. graecizans, of which subsp. *graecizans* is the narrow-leaved race (see the key), is characterised by its axillary inflorescences; by its bracteoles being shorter than the perianth; and by the ♀ perianth-segments being shorter than the fruit.

As Dandy & Melderis have pointed out (Fernandes, 1957, 191), the type in the Linnaean Herbarium (No. 1117.3) agrees with what has been hitherto usually known as *A. angustifolius* Lam.

subsp. *SYLVESTRIS* (Vill.) Brenan, *comb. nov.*

Amaranthus sylvestris Vill. (1807) 111; Fernandes, 1957, 192.

Amaranthus graecizans L. var. *sylvestris* (Vill.) Asch., 1867, 176; Briquet, 1910, 471, as "*silvestris*"; Aellen, 1959, 500, fig. 231 (p. 472), fig. 242f, g, s, t, (p. 505).

Amaranthus angustifolius Lam. "proles" *sylvestris* (Vill.) Thell., 1914, 300, as "*silvester*."

Amaranthus angustifolius Lam. var. *sylvestris* (Vill.) Thell., 1923, 222; Kloos, 1953, 324; Priszter, 1953, 197, t, 26, fig. 41a (p. 203), t. 38, fig. 56d (p. 232).

Amaranthus angustifolius Lam. subsp. *sylvestris* (Vill.) Heukels, 1934.

The geographical range of subsp. *sylvestris*, which is easily distinguished from subsp. *graecizans* by, among other things, its broader leaves, is similar, as is its occurrence in Britain.

Although treated by Fernandes (1957) as a species, I do not find the distinguishing characters given by Thellung (1914) to be sufficiently constant and well-marked to justify that view. Thellung considered *graecizans* and *sylvestris* as "proles" of a single species, which seems nearer the truth. For the above reason also I have been forced to eliminate from the key certain alleged distinctions given by Thellung (1914): notably the shape of the bracteoles (lanceolate in subsp. *graecizans*, ovate-lanceolate in subsp. *sylvestris*), the form of the midrib of the ♀ perianth-segments (broadened towards apex in subsp. *graecizans*, not or scarcely so in subsp. *sylvestris*), and the shape of the keel of the seeds (usually blunt in subsp. *graecizans*, sharp in subsp. *sylvestris*). I do not find any of these characters sufficiently clear or constant to be of much help in identification.

Amaranthus angustifolius Lam. "proles" *polygonoides* (Moq.) Thell., 1914, 308, similar to subsp. *graecizans*, but with narrow lanceolate and long-pointed ♀ perianth-segments with an apical spinule (0.25-) 0.3-0.75 mm. long (as against 0.25 mm. or less), and bracteoles of similar shape with often even longer points, has not so far been found in Britain, but should be looked for.

14. *AMARANTHUS MACROCARPUS* Benth., 1870, 216; Thellung, 1914, 311; Aellen, 1959, 499, fig. 230 (p. 472).

Amaranthus macrocarpus Benth. var. *melanocarpus* Thellung, 1914, 311; Kloos, 1953, 325.

A. macrocarpus is a native of Australia. Although Thellung and Kloos have both used the varietal name *melanocarpus*, it is in fact strictly synonymous with typical *macrocarpus* and if a varietal name is used it should be *A. macrocarpus* Benth. var. *macrocarpus*. It has been found only rarely in England, as a wool-alien:—

V.c. 12, N. Hants.: Blackmoor, 24 Oct. 1959, J. E. Lousley W 1337. V.c. 37, Worcs.: in cabbage-field, Pinvin, 4 Sept. 1955, C. M. Goodman 430 in *Herb. Lousley* W 168. Shoddy field, Evesham, Charlton, Sept. 1959, C. W. Bannister, & 21 Sept. 1959, C. W. Bannister in *Herb. Lousley* W 986 & 19 Sept. 1959, C. M. Goodman 1856 in *Herb. Lousley* W 1039.

A. macrocarpus is outstanding on account of its glabrous stems, emarginate leaves, axillary inflorescences, 3 perianth-segments in both sexes, and elongate fruits 2-3 times as long as the perianth and (in var. *macrocarpus*) blackish when dry.

15. *AMARANTHUS DEFLEXUS* L., 1771, 295; Thellung, 1914, 313; Covas, 1941, 341, fig. 6 A-F (p. 344); Kloos, 1953, 326; Priszter, 1953, 205, t. 29, fig. 46a (p. 211), t. 38, fig. 56e (p. 232); Aellen, 1959, 504, fig. 235 (p. 473).

A. deflexus is, according to Thellung (1914, 318), South American in origin, but has now become naturalised in North America, the Mediterranean region, and elsewhere. In Britain it is a rather rare alien, especially near docks, and sometimes introduced with wool-manure.

A. deflexus is remarkable among the other species of the genus mentioned in this paper in being a perennial. It is further distinguished by the stems being hairy above, acute leaves, usually partly terminal inflorescences, and by its indehiscent fruits longer than wide, inflated and twice as long as the perianth.

16. *AMARANTHUS LIVIDUS* L., 1753, 990; Thellung, 1914, 319; Fernandes, 1957, 193; Aellen, 1959, 505, Fig. 236 (p. 473).

subsp. *LIVIDUS*

Amaranthus blitum L., 1753, 990; Fernandes, 1957, 189-194.

- Amaranthus ascendens* Lois., 1810, 141; Merrill, 1936, 611; Priszter, 1953, 214, t. 31, fig. 48a (p. 219), t. 38, fig. 56g (p. 232).
Amaranthus blitum L. var. *ascendens* (Lois.) DC., 1813, 4.
Amaranthus lividus L. "proles" *ascendens* (Lois.) Thell., 1914, 321.
Amaranthus lividus L. var. *ascendens* (Lois.) Hayward & Druce, 1919, 177; Thellung, 1923, 223; Covas, 1941, 345, fig. 6 I-J (p. 344); Kloos, 1953, 327, fig. 38 (p. 329); Aellen, 1959, 506, fig. 242 Aa-k, 242B (p. 505).
Amaranthus lividus L. subsp. *ascendens* (Lois.) Heukels, 1934, 169.
Amaranthus ascendens Lois. var. *lividus* (L.) Priszter, 1953, 221.

A. lividus is widespread through the tropics and warmer regions of the world. It is distinguished by being quite glabrous and having normally emarginate leaves, inflorescences usually partly at least terminal, and indehiscent fruits about $1\frac{1}{2}$ times as long as the perianth.

As pointed out by Dandy & Melderis (see Fernandes, 1957), although the type of *Amaranthus blitum* L. in the Linnaean Herbarium (No. 1117.14) is certainly *A. lividus* subsp. *lividus*, the name *A. blitum* has become, owing to repeated misapplication, such a source of confusion and ambiguity that it would be unwise to resurrect it.

Typical *A. lividus* is at present a decidedly rare alien in Britain, usually on rubbish-tips. Judging from the number of old specimens in herbaria, it was more frequent in the nineteenth century than now.

subsp. *POLYGONOIDES* (Moq.) Probst, 1949, 74.

Euxolus viridis (L.) Moq. var. *polygonoides* Moq. 1859, 274.

Amaranthus ascendens Lois. var. *polygonoides* Thell. ex E. H. L. Krause in "Mittheil. Philom. Ges. Els.-Lothr. IV. 3. 1910 S. 372 (1911)" *vide* Thellung, 1914, 320; not seen.

Amaranthus lividus L. "proles" *polygonoides* (Moq.) Thell., 1914, 320.

Amaranthus lividus L. var. *polygonoides* (Moq.) Thell., 1920, 574; Aellen, 1959, 506 (as "var. *polygonoides* (Zollinger) Thell.").

Amaranthus ascendens Lois. subsp. *polygonoides* (Moq.) Priszter, 1953, 221 (as "ssp. *polygonoides* (Zollinger) Thellung, apud E. H. L. Krause . . ."), t. 31, fig. 48a (p. 219).

A. lividus subsp. *polygonoides* is found, according to Thellung (1914) 321, in the tropics of both hemispheres. In Britain it is a very rare alien. In B.E.C. 1919 Rep., 574 (1920), a specimen from "cultivated fields about London, circa 1822, W. Blake, in *Hb. Druce*" was said to have been so identified by Thellung. It has also occurred more recently, as follows:—

V.c. 21, Middlesex: waste ground, Hackney Marshes, 23 Sept. 1913, [J. E. Cooper] in *Herb. Kew.* V.c. 34, W. Glos.: Avonmouth Docks, 30 Sept. 1928, C. I. Sandwith in *Herb. Sandwith*.

17. AMARANTHUS VIRIDIS L., 1763, 1405.

Amaranthus gracilis Desf., 1804, 43; Thellung, 1914, 335; Covas, 1942, 343, fig. 5 C-D (p. 342); Kloos, 1953, 330; Priszter, 1953, 223, t. 33 (p. 224), t. 38, fig. 56 i (p. 232); Aellen, 1959, 503, Fig. 234 (p. 473).

The nomenclature of this species has been much misunderstood. As Merrill (1935) has pointed out, the type-specimen of *A. viridis* in the Linnaean Herbarium (No. 1117.15) is conspecific with *A. gracilis* Desf.; see also his elaborate paper on the application of the binomial *Amaranthus viridis* L. (Merrill, 1936, 609-612), where there is a photograph

of the Linnaean type (Fig. 2, p. 610).

A. viridis is a pantropical species, occurring as an occasional alien in Britain, introduced with wool-manure and also by other means. It is easily recognised by its partly terminal inflorescences and strongly muricate fruits shorter than, or about as long as, the perianth.

18. *AMARANTHUS CRISPUS* (Lesp. & Thév.) N. Terracc., 1890, 188; Thellung, 1914, 340; Covas, 1941, 343, fig. 5 C-D (p. 342); Kloos, 1953, 332; Priszter, 1953, 225, t. 38, fig. 56j (p. 232); Aellen, 1959, 491, fig. 217 (p. 471).

Euxolus crispus Lesp. & Thév., 1859, 656.

A. crispus is native of the Argentine, but has been for some time naturalised in southern Europe and locally in the United States. It has been found only once in Britain, as a wool-alien :—

V.c. 37, Worcs.: in crop of beans, Fladbury, 28 Aug. 1958, C. W. Bannister in *Herb. Lousley*.

A. crispus is easily recognised by its prostrate stems, small crisped-margined leaves, axillary inflorescences, 5-merous perianths, obovate-spathulate ♀ perianth-segments, and muricate fruits.

19. *AMARANTHUS STANDLEYANUS* Parodi ex Covas, 1941, 339.
[*Amaranthus vulgatissimus* sens. Thell., 1914, 343, et auct. eur. al., e.g. Kloos, 1953, 333; Aellen, 1959, 493, fig. 219 (p. 471); non Spegazz.].

Covas (1941) has pointed out that *Amaranthus vulgatissimus* was misinterpreted by Thellung and has been used in the same wrong sense by authors dealing with adventive plants in Europe. Covas gives the following key :—

Perianth-segments of the ♀ flowers markedly spatulate, with the base markedly attenuate and almost linear and not more than 0.3 mm. wide :

Leaves undulate-crenate on margin

A. crispus

Leaves ± flat and entire on margin

A. standleyanus

Perianth-segments of the ♀ flowers oblong-spathulate, with the base somewhat attenuate and more than 0.3 mm. wide

A. vulgatissimus

The plant hitherto wrongly known in Britain as *A. vulgatissimus* Spegazz. is in fact *A. standleyanus*, a species from the Argentine. It is a rare alien in Britain, usually near docks or introduced with wool-manure. It is easily distinguished by its flat-margined leaves, usually partly terminal (but sometimes wholly axillary) inflorescences, 5 spatulate ♀ perianth-segments, and indehiscent fruits.

20. *AMARANTHUS MITCHELLII* Benth., 1870, 214; Aellen, 1959, 493, fig. 220 (p. 471).

This remarkable species, a native of Australia, has been recorded once in Britain, as a wool-adventive :—

V.c. 12, N. Hants.: Blackmoor, 11 Oct. 1959, J. E. Lousley W 1331.

It is outstanding on account of its flat-margined, elliptic-lanceolate leaves, entirely axillary inflorescences, 5-merous perianths, and remarkably spatulate ♀ perianth-segments with slender claw and broad spreading lamina, whose green midrib is remarkably broadened and branched in the laminar part so as to form a green patch in the middle of each of the perianth-segments. The fruit is longitudinally ribbed and with smooth swollen style-bases. Altogether it is unmistakably distinct from any of our other species.

21. *AMARANTHUS CLEMENTII* Domin, 1921, 630.

Amaranthus pallidiflorus F. v. Muell. var. *viridiflorus* Thell., 1928, 60.

[*Amaranthus pallidiflorus sensu* Aellen, 1959, 490 *quoad descr. pro parte et fig.* 215 (p. 470); non F. v. Muell.]

A. clementii, although it keys out near *A. quitensis* H.B.K. on account of the leafless apical part of its inflorescence, 5 spathulate ♀ perianth-segments, and circumscissile fruits, is probably not at all closely related to *A. quitensis*. It seems to be akin rather to *A. standleyanus* Parodi ex Covas, from which it is separated by the circumscissile fruits and the remarkable broadening and branching of the green midrib of the ♀ perianth-segments, so that there seems to be a green area in the spathulate part of each segment; also to *A. mitchellii* Benth., which is completely distinct from *A. clementii* in having the inflorescence altogether axillary.

A. clementii is a native of Australia which has occurred once in Britain, as a wool-advective, as follows:—

V.c. 37, Worcs.: Charlton, 19 Sept. 1959, C. M. Goodman, 1859 in *Herb. Lousley* W 1040.

Although Thellung (1928) and Aellen (1959) have treated this plant as a variety of *A. pallidiflorus* F. v. Muell. (1859), the distinguishing characters seem so clear and constant in Australian material that I prefer to accept Domin's opinion of it as a distinct species. The leaves of *A. clementii* are narrow and lanceolate to linear-lanceolate, while those of *A. pallidiflorus* are much broader in relation to their length and mostly elliptic to rhombic-elliptic. Furthermore, the ♀ perianth-segments of *A. pallidiflorus* have a thin green midrib neither branched nor broadened above, and also narrower claws than in *A. clementii*.

22. *AMARANTHUS TUBERCULATUS* (Moq.) Sauer, 1955, 18; Aellen, 1959, 509.

Acnida tuberculata Moq., 1849, 277.

This species is one of our four alien amaranths which are dioecious. Their distinguishing features are given in the key above. It is a native of the United States, and has been found only rarely in Britain, as follows:—

V.c. 34, W. Glos.: Avonmouth Docks, 12 Oct. 1958 & 20 Sept. 1959, C. I. & N. Y. Sandwith in *Herb. Sandwith*; 4 Oct. 1959, N. Y. Sandwith & D. McClintock in *Herb. Lousley*.

The 1958 specimen, which like the 1959 one is ♀, has been determined by Dr. Sauer himself.

A. tuberculatus and *A. tamariscinus* have been often placed in a separate genus, *Acnida* L., but Sauer (*l.c.*) has given cogent reasons for not maintaining it. Cytological support for this view is given by Grant (1959).

23. *AMARANTHUS TAMARISCINUS* Nutt., 1837, 165; Sauer, 1955, 26; Aellen, 1959, 509.

A. tamariscinus, like *A. tuberculatus*, is a dioecious species native of the United States. Like the latter species also, it has been found only rarely in Britain, and strangely enough in the same locality:—

V.c. 34, W. Glos.: Avonmouth Docks, grown on from root collected there on 4 Aug., 14 Sept. 1957, J. E. Lousley in *Herb. Lousley*; do., from plant collected there on 31 Aug. 1959, 14 & 28 Oct. 1959, J. E. Lousley in *Herb. Lousley*.

The specimens are ♂.

24. *AMARANTHUS PALMERI* S. Wats., 1877, 274; Sauer, 1955, 31; Aellen, 1959, 509, fig. 237-8 (p. 474).

This remarkable dioecious species is very easily distinguished from its two relatives, *A. tuberculatus* and *A. tamariscinus*, by the well-developed perianth of its ♀ flowers with conspicuously spatulate inner segments, also by the longer bracts. The unusually long petioles, often equalling or exceeding the leaf-blades, are distinctive. It is a native of the United States and Mexico, recorded only in two British localities where, however, it appeared in some plenty at Avonmouth.

V.c. 12, N. Hants.: Alton, a single plant in sidings at railway station where woolshoddy had been unloaded, 18 Oct. 1959, *Miss V. Leather & Miss M. McCallum Webster* in *Herb. Kew.* (♂). V.c. 34, W. Gos.: Avonmouth Docks, 29 Aug. 1959, *Miss M. McCallum Webster*, 2063 (♂), 2064 (♀) in *Herb. Kew.* & 20 Sept. 1959, *C. & N. Sandwith* (♂), 4 Oct. 1959, *N. Y. Sandwith & D. McClintock* in *Herb. Lousley* (♂ & ♀), 11 Oct. 1959, *Mrs. N. Saunders* in *Herb. Lousley* (♂ & ♀).

A plant from Avonmouth (11 Oct. 1959, No. 2068 in *Herb. Kew.*) each of whose leaves has about the middle on the upper side a white mark resembling an inverted V, was collected by *Miss McCallum Webster*. It is immature, there are no terminal spikes, but a few female flowers in the leaf-axils. I suspect it to be a form of *A. palmeri*, of which it has the general habit and long petioles, but its identity is not certain without more evidence.

25. *AMARANTHUS WATSONII* Standl., 1914, 505, as "*watsonii*"; Sauer, 1955, 36; Aellen, 1959, 510.

Amaranthus watsonii, yet another of the extraordinary series of dioecious amaranths that has unexpectedly appeared at Avonmouth Docks, Bristol, during the past three years, is clearly more closely related to *A. palmeri* than to other species in this group. It is the only one of our dioecious amaranths with strong pubescence, and its grey-green colour in the field is in strong contrast to the bright green of *A. palmeri*. The other distinguishing features are given in the key. *A. watsonii* is native of Mexico (Baja California and Sonora) and the United States (California and Arizona).

V.c. 34, W. Gos.: Avonmouth Docks, 3 Oct. 1959, *C. & N. Sandwith* (♂ and ♀), 11 Oct. 1959, *Miss McCallum Webster* 2066 in *Herb. Kew.* (♂).

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A RUSSIAN *ALCHEMILLA* IN SOUTH SCOTLAND

By M. E. BRADSHAW and S. M. WALTERS

Whilst botanising in south Scotland in 1956 M.E.B. found a few small colonies of an unfamiliar species of the *Alchemilla vulgaris* aggregate at two points about half a mile apart near Bowhill, west of Selkirk (v.c. 79). A return visit in August 1957 showed that the plant was abundant in dense stands by paths and roads of the Bowhill estate (National Grid ref. 36/4227).

The plant did not correspond to any of the known Scandinavian or central European species, but reference to the *Flora U.R.S.S.* indicated that it probably belonged to the section *Nemorales* of Juzepczuk, in particular *A. tythantha* Juz. Meanwhile herbarium material sent to Professor W. Rothmaler had been identified by him as "the remarkable *A. multiflora* Buser ex Rothm., native country unknown, which I observed cultivated in Germany, Austria and Switzerland" (*in litt.*). The Selkirk plant certainly agreed well with plants of *A. multiflora* in the Cambridge Botanic Garden grown from seed supplied earlier by Rothmaler. Obviously the question arose, was there any connection between *A. tythantha* Juz. and *A. multiflora* Bus. ex Rothm.? Further investigation revealed that they were in fact synonyms, as is explained on the herbarium sheets of the former distributed by Juzepczuk (first seen by S.M.W. in the herbarium at Vienna and now available in the British Museum (Natural History)); and the Selkirk plants were found to agree well with the distributed material of *A. tythantha* Juz.

The history of the name *A. multiflora* is an interesting one. Buser knew the plant in the Botanical Garden at Vienna, where it was in cultivation in 1887; there is material determined as *A. multiflora* by Buser in both the University Herbarium and the Natural History Museum at Vienna. Rothmaler had seen this material, and also knew the plant in cultivation at the Berlin Botanic Garden, and on this basis published the name as *A. multiflora* Buser ex Rothm. (1939) with a description and a note on what was known of its history. The native home of the plant was unknown to Rothmaler, though Buser had indicated that it might have come from the Crimea. This was confirmed by Juzepczuk, who recognised the cultivated plant as being the same as his *A. tythantha*, an endemic of the Crimea which he described and published in 1933.

As the most readily available description of *A. tythantha* is in Russian (Komarov, 1941), a description of the wild British material follows (see plate 17).

Plant medium-sized, 20–50 cm. Lower part of inflorescence and petioles densely clothed with spreading, usually *slightly deflexed hairs*, upper branches, pedicels and flowers glabrous. Leaves round, with narrow basal sinus (c. 10°–40° (90°)), *densely hairy on both sides*, late summer leaves less hairy but not glabrous; lobes usually 9, rounded, sometimes straight-sided; teeth acute, porrect; cauline leaves rather large. Flowers yellow-green, *small*. (1.5–2.5 (–3) mm. diam.).

The plant is easily recognised by the combination of very hairy leaves and very small flowers, together with the almost invariable presence of some *downwardly-directed hairs* among the dense spreading pubescence of stem and petiole.

Herbarium material is deposited in the herbarium at the University of Durham, Durham, and at the Botany School, Cambridge.

In the Bowhill area *A. tythantha* is common along the roads and paths through the

woods immediately around the house. These woods contain many conifers, but the *Alchemilla* localities are not heavily shaded, and in some places the plants are in open rough grassland. A few stands grow amongst roadside trees and shrubs just south of the bridge over the R. Yarrow. The species forms dense stands resembling *A. xanthochlora* Rothm. and *A. acutiloba* Bus. The following associated species were recorded in a metre quadrat containing *A. tythantha* by a road in a mixed oak-elm wood west of Bowhill. Figures are Domin scale (1-10) abundance - cover estimates

<i>Dactylis glomerata</i>	7	<i>Ranunculus repens</i>	1
<i>Alchemilla xanthochlora</i>	4	<i>Filipendula ulmaria</i>	1
<i>Phleum pratense</i>	2	<i>Plantago major</i>	1
<i>Heracleum sphondylium</i>	2	<i>Rumex conglomeratus</i>	1
<i>Geranium sylvaticum</i>	1	<i>Agrostis tenuis</i>	1

(1 = less than 4% cover, rare; 2 = less than 4% cover, scattered; 4 = 4%—10% cover; 7 = 34%—50% cover.)

More recently (1959) the species was found on another estate near Duns (v.c. 81), also in South Scotland, but no details of the record are available.

The origin and history of the plant in Scotland is uncertain. The head-gardener at Bowhill had no record of the plant in cultivation in the garden. Among the '*Alchemilla vulgaris*' material in cultivation at the Royal Botanic Garden, Edinburgh, is a plant which is referable to *A. tythantha*. The cultivated material shows slight differences from the Selkirk plant, but these could be due to environmental modification, and an origin via the Edinburgh Botanic Garden seems very plausible.

It is probable that the plant is more widespread in Britain, and it should be looked for. A tour of the large estates in south Scotland may produce a novel and interesting distribution map!

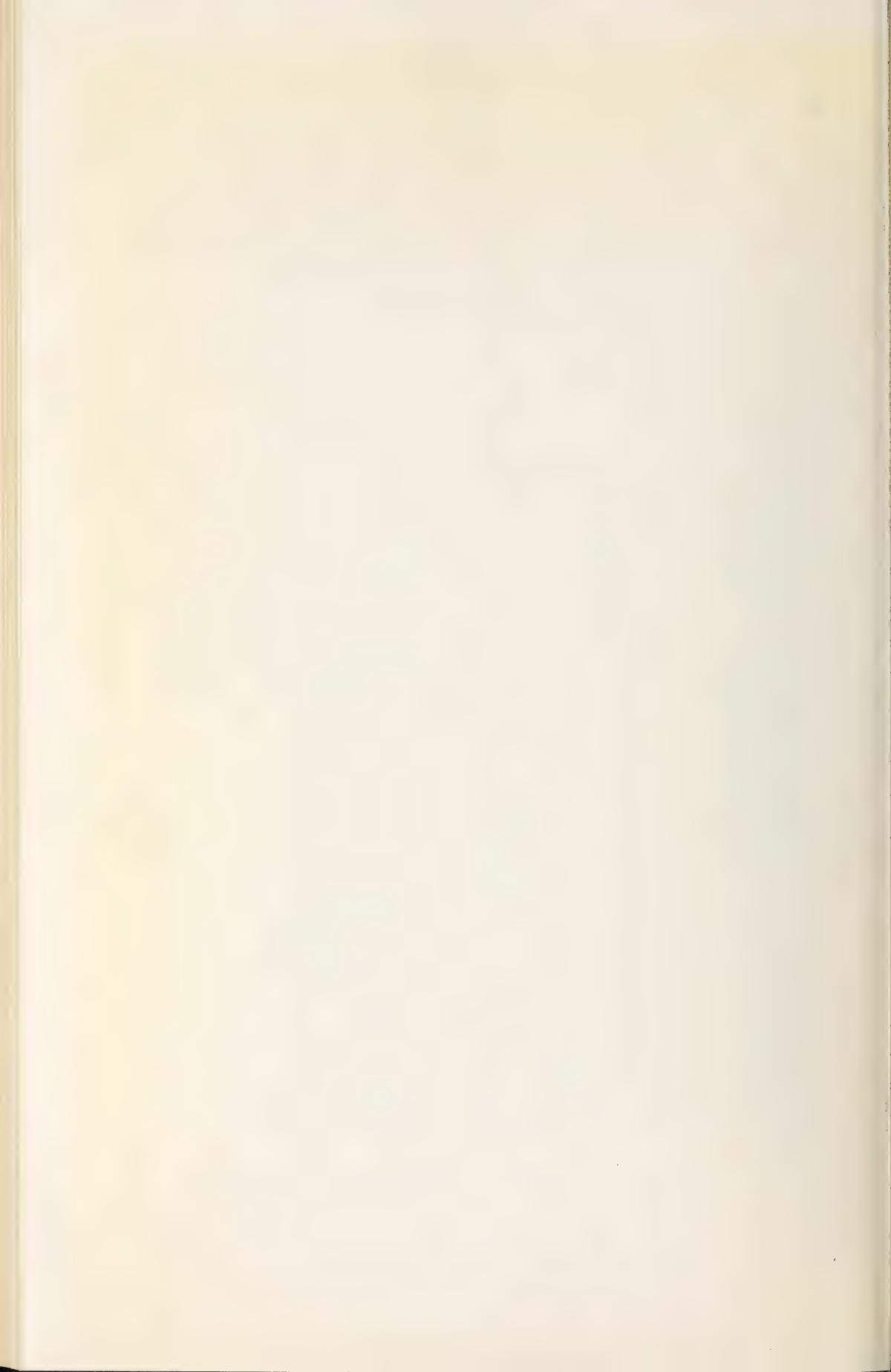
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PLATE 17.



Alchemilla tythantha Juz. whole plant, and unattached leaf from a larger plant ($\times \frac{1}{2}$) A. part of petiole ($\times 5$), B. part of inflorescence ($\times 2$). Bowhill, Selkirk, 1957.



HINTS FOR HARD-PRESSED COLLECTORS

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“Anybody can collect” is an opinion that trips too readily from the biologist’s tongue. Anyone, it is true, *can* collect herbarium specimens – after a fashion. And a quick look at our great herbaria will show how badly people have often done it: plants snatched on the way to Lhasa, or decapitated by British Consuls riding fast to Trebizond. But that is not good enough. If our collections are to be of lasting scientific value, we need to enrich our herbaria, not to fill them with scraps. The herbarium still provides the foundation for practical classification and nomenclature. The techniques of experimental taxonomy cover a very limited part of the World’s flora. Population studies undertaken in a limited area give us less idea of the variability of a widespread species than we can obtain by going through the material in a big herbarium. It is only in the herbarium that we can usually compare all the related species of a genus in the same place, in the same state, and at the same time. The collector can play an important part by seeing that his herbarium specimens provide as much information as possible, and thus form a sound basis for further research.

Many biologists who are not professional collectors get abroad these days, and are often willing (or can be persuaded) to collect herbarium material. It is for them that these notes are primarily intended. My own collecting experience has been acquired mainly in the Middle East, by trial and error, and I hope to provide a few hints that may not be found in other published work on the subject. Those who intend to collect in the tropics, or to specialise in certain groups, should read *Instructions for Collectors No. 10, Plants*, a handbook produced by the British Museum (1957) that contains much staid and valuable information. The Royal Botanic Gardens, Kew, distribute to their collectors a duplicated sheet of more concise hints. A useful article on drying by artificial heat (including references to earlier papers) has been written by J. A. Steyermark in *Rhodora*, **49**, 220-277 (1947).

HOW AND WHAT TO COLLECT

Even in relatively well-botanised countries there are often regions, or habitats, that have been neglected, or only visited at particular seasons. Often the commonest plants (particularly if they are inconspicuous or difficult to press) are poorly represented in herbaria, so that it may be difficult for the botanist to obtain reliable information about their distribution or variability. In little-known regions good material of all species is usually welcome, but if time is a limiting factor it is advisable to seek advice from our National Herbaria (Kew, British Museum and Edinburgh) on what is most required from the area you intend to visit. It is a great deal better to collect a little material well than to press a large amount of scrappy, poorly annotated specimens. It is when one attempts to collect nearly everything (as I do myself) that one is apt to get into difficulties. The limit to the amount one can collect, if one devotes full time to it, is usually set by the number of plants one can successfully press, label and dry. And that will depend not only on the weather, but also on one’s stamina and constitution. Some collectors get up at dawn, others label and change their presses late into the night, but few can do both

for long. As the painter Fuseli remarked, "Damn Nature, she always puts me out!"

Herbarium specimens should, as far as possible, be representative of their populations. Collect to show the range of variation, but if any particular variant is unusual this fact should be indicated in your field notes (e.g. "shade form"). If this is not done an aberrant specimen may mislead the systematist. Whenever possible, specimens should be collected in flower and fruit from the same place – if possible even from the same plant. In some families (e.g. Compositae, Cruciferae, Chenopodiaceae) the fruit is generally more useful for identification than the flower. In herbaceous plants the rootstock should be collected whenever possible – and the bulb, corm or tuber if it has one. Fleshy underground parts can be sliced open to facilitate drying. Bulbs can be killed by plunging them in boiling water, or by immersion in alcohol. Boiling water, however, is unsuitable for most corms (e.g. *Colchicum*). These store starch which swells up and gives birth to a fine crop of mildew in the press; it is like trying to press a boiled potato. Thick stems can be slit open vertically. Tall bulky plants like *Verbascum* and *Onopordon* will have to be sectioned before they can be pressed, the basal leaves, and the middle and upper portion of the stem (with leaves attached) being placed on consecutive sheets. Paper pads can be inserted to even up the pressure on leaves and flowers. On bulky specimens, however, delicate corollas usually shrivel unless they are separately pressed. This can be conveniently done between sheets of diaphanous toilet paper which acts as a miniature "fimsy" (see below).

Showy Monocotyledons deserve special treatment which will improve their state of preservation and facilitate examination in the herbarium. When perfectly fresh, the flowers of *Iris* (which are readily reduced to a grey mush in the press) can be taken to pieces and their parts pressed separately, their form and even colour being quite well preserved by this means. Flowers of *Crocus* and *Tulipa* can be opened out to expose the diagnostic genitalia. In Orchids and other groups in which flower shape is very important for identification, pressed specimens should be supplemented by flowers preserved in tubes of "spirit." Succulents (e.g. *Sedum*) can be conveniently identified if leafy flowering shoots are preserved in the same way. The preservative used at Kew is made up of industrial spirit (11 parts), 40% formalin (1 part), water (8 parts) and glycerine (1 part). "Pickled" material should bear the same number as the dried specimens and it is essential that full colour notes should be taken. Colour photography should become increasingly useful to the taxonomist, especially in the petaloid Monocotyledons, but, like spirit material, the transparencies should be closely correlated with herbarium specimens. Advice on collecting special groups (including aquatics and Cryptogams) will be found in the British Museum handbook.

A vasculum, if one is collecting a large amount, is of little use except for sandwiches. In hot countries it turns into an oven, and when climbing rocks it can swing round to electrocute your elbow. A good method is to collect into a portfolio with cardboard covers holding newspaper folders or fimsies. A portfolio is more conveniently carried than a sharp-angled wooden press, and the plants will not get a chance to wilt if pressed as soon as collected. If webbing straps are attached to the portfolio, it can be carried on the back like a rucksack. It is essential to press at once if the petals are to be retained in such genera as *Papaver*, *Helianthemum* and *Linum*. It is usually possible to collect several species at the same spot, and these can be enclosed in a common folder and a written slip inserted to remind us of their locality, habitat and altitude which should be entered in the field note book at the end of the day. If a great deal of ground is covered, some form of field labelling is essential; how much will depend on the collector's experience and visual memory. Collectors previously unacquainted with the flora, or who are concentrating on critical genera, would be well advised to label as much as they possibly

can in the field. Often, however, it is not practicable to stop and press every plant as we collect it; the weather may be against it, or we may be pushed for time. In that case I would strongly recommend the use of a large, strong, plastic bag about 3 ft. deep. When empty this can be folded into the pocket. If closely wrapped round the plants we put in it, the specimens will remain fairly fresh all day – and even all night as well. A little water can be sprinkled inside to raise the humidity.

A word about collecting tools will not be out of place here. Although a steel fern-trowel is a time-honoured implement, I prefer a small “chopper” for collecting in the Mediterranean where soils are very stony and baked hard during the summer. The blade, about 9 in. long, has a cuneate cutting edge at one end and two prongs at the other, a 1 ft. handle of strong wood being wedged in the hole in the middle. This makes a very efficient tool which can be used with the minimum of effort: the cutting edge can be used for digging, chopping up portions of spiny cushion plants, or cutting up the stems of thistles and mulleins into suitable lengths for the press; the prongs are very useful for prizing up stones and for collecting bulbs without slicing them in half. Iron choppers of this type are used by Turkish peasantry but the metal is too readily blunted; it is preferable to get them made of steel in Britain. A large strong knife is always a handy tool, and a small pair of secateurs is advisable for cutting branches – thorny Rosaceae are painful to tackle without it.

FIELD NOTE BOOKS

Many National Herbaria provide collectors with their own field note books, but when one is attempting to press a great deal I find that these take too long to fill up. I have adopted the use of a large, ledger-sized book (17 $\frac{3}{4}$ in. \times 12 $\frac{1}{2}$ in.) with stiff covers. In this columns are ruled to accommodate the following data:

1. *Number of plant.* This should preferably be a straight serial number, so that it is not necessary for a taxonomist to give the country or date when he needs to cite your specimen. (When the labels come to be typed, the name of the country will be placed at the head of the label, and the collector's name will precede the number.)
2. *Name of plant.* When the species is not known, the genus or family should be given whenever possible.
3. *Province* – or whatever the major divisions of the country are that you wish to use.
4. *Locality.* This should be as precise as possible, and should include a place name that is readily found on the map.
5. *Altitude* (preferably in metres). The altitude at which the gathering was actually made should be given here. If you wish to indicate the species' altitudinal range, this should be given in parenthesis after the altitude of the gathering, or be transferred to the heading 'Remarks.'
6. *Habitat*, which should include the type of terrain (e.g. sandy fallow fields) and preferably some indication of the community (e.g. *Quercus coccifera* maquis).
7. *Remarks.* These should include notes on any feature of the gathering that may not be apparent from the dried specimen in years to come. Flower colour should be given and notes on the plant's duration and habit (e.g., biennial or perennial, height if a tree or shrub, stems erect or ascending). Notes on frequency and variability can be given here, and remarks on properties and the vernacular name if correctly ascertained.
8. *Date of collection.*

The advantage of this type of note book is that it saves a great deal of time because, instead of repeating the details for many plants collected in the same place, "ditto" signs can be given. If one's writing is legible, anyone can type labels directly from the field book. The book should be written in pencil (not indelible), and must have very stiff covers if it has to be pushed into a rucksack. The only disadvantage of this type of note book is that, if it is lost, all your data are lost and the collection will be almost useless. Never be parted from your note book till both collection and book are safely home!

Useful though it is to have biological information about each gathering, we must restrict the amount that is entered in the main note book; if we do not, the labels compiled from it may be so large that they will not leave room for the mounted specimen.

PRESSES, STRAPS AND PAPER

I have always used wooden lattice presses containing drying paper of the standard Kew size. The latter, when folded ready for use, is about the size of the sheet on which the specimen will be mounted, i.e. $16\frac{1}{3}$ in. \times $10\frac{1}{2}$ in. It is very important, if you are travelling rough, that the press should be scarcely bigger than the paper which it contains. This not only insures safer transport of the specimens, but also curbs a temptation to press specimens that will be too big for the mounting paper.

There is no doubt that thick, hand-made paper (as used by the Kew Herbarium) is by far the best drying material for use in the field. The life of ordinary blotting paper is very much shorter. It is preferable to use the drying paper folded double and to take much more than you think you will need. There is nothing more thwarting for a keen collector than a shortage of dry paper – it is much commoner than a shortage of specimens. The paper should be changed every day (to remove the moisture absorbed from the plants), and it is advisable to have enough for at least two complete changes in case bad drying conditions form a bottle-neck from which only mouldy specimens may return. In the case of a crisis, newspaper can be successfully used for drying. It is preferable, however, to alternate this with drying paper, because newspaper lets through much less air than the latter and is less absorbent. Cardboard can be used to separate thick specimens which can also be laid head to tail to even out the pressure in a bulky press. The type of corrugated cardboard with a flat surface on both sides is ideal for the purpose; it is very light and allows air to circulate through the press. One should preferably carry enough presses to avoid having them more than 3 in. thick; the thinner they are the quicker they dry. If short of presses, a single lattice placed in the middle of a fat press helps drying very considerably, and so does the moving of wet specimens from the middle of the press to near the outside.

Webbing straps with reliable spiked buckles are probably best, but unless the webbing is strong and of a close weave the straps may tear and allow the press to fly open if carelessly handled. Irreparable chaos can result from a broken strap or buckle, and herbaria should never provide collectors going abroad with any but the best straps. In dry climates leather straps are apt to snap unexpectedly, and are not infrequently stolen.

The transport of presses always needs care. At such times the straps should always be tight – but not so tight as to risk snapping. Sometimes a press tumbles off the top of a bus, or falls from a horse scared on a steep mountain side. If the lattice is much bigger than the paper, the press will be smashed and the contents scattered over the countryside. There is much to be said for carrying one's presses in hessian sacks – indeed, on horseback it is almost essential to enclose them in some way and to cover them with tarpaulins in rainy weather.

I am often asked how many presses and how much paper a collector should take with him. A full-time collector, especially if he has assistance with changing and drying

papers, can collect at least 1,000 numbers a month in triplicate – say 3,000 sheets. In fine Mediterranean weather the average drying time per specimen is about a week, but 10 days or so in wet weather. (Succulents and many bulbs, unless killed before pressing, will take longer). That means that there may be as many as 1,000 sheets of specimens in the press at the same time. This will necessitate the use of at least 2,000, preferably 3,000, sheets of drying paper. At least 20 presses will be required, and up to 30 during the summer months when species tend to be bulkier than in the spring.

DRYING THE PRESSES

Whenever possible the presses should be stood in the sun or wind to dry, or be placed near any gentle artificial heat available. Stand them on end. The straps should be kept tight for the first few days, though not so tight that organs are crushed. When the specimens are almost dry, the pressure can be slackened to “finish them off.” The drying paper should, of course, be changed every day, especially during the first few days. If time allows, a double change the first day is desirable. If for some reason it is impossible to change the paper for a day or two, the press should *not* be exposed to strong heat – either from the sun or fire. The result is likely to be a compost heap! Presses, if they are stood in hot sun, should be turned round from time to time to prevent unilateral drying. There comes a moment, when one’s specimens are nearly dry, when they easily “go back” if they are not changed into really dry paper. Fleshy halophytes should be dried in a separate press as they tend to keep other specimens moist. If travelling by bus or car, drying is speeded up if the presses are securely tied to the luggage rack; or a press may be wedged between the mudguard and the bonnet.

Quick drying, to avoid decay of the tissues, is the secret of good pressing, and everything should be done to achieve it. It is, however, possible to overdry specimens so that they become so brittle that they break up when handled.

I most strongly advocate the use of *flimsies* for drying all plants except the bulkiest or most spiny specimens. These are folders, the same size as the drying paper, and made of very thin, absorbent paper. Newspaper is a good substitute. The specimen is pressed straight into the flimsy and need not be handled again until it is dry – except that, at the first change, many folded leaves or even petals can be straightened out, a process which makes all the difference to the appearance of the finished article. The freshly collected specimen should have its field number put in the flimsy with it. The safest method is to write the number on a jeweller’s tag so that it can be readily attached to the specimen by the cotton loop it bears. When changing papers, only the thick papers need to be changed, the specimen being moved on to dry paper in its original (still damp) flimsy. To begin with, when specimens are very damp and provided they are not so delicate that they stick to the paper, drying will be accelerated if drying paper is slipped inside the flimsy as well as placed between successive flimsies. The use of flimsies cuts out the handling of specimens which can seriously damage plant material. It also means that the changing can be done in half the time, and can be safely carried out by any careful person who will lend a hand. It does, however, add to the boredom of the chore, because one sees little of the specimens until they are dry. One should resist peeping at thin, delicate corollas during paper-changing; the petals of *Iris* and *Crocus*, for instance, curl up as soon as the flimsy is opened.

When the specimen is dry there is no need to remove it from the flimsy. Its number should be written on the outside of the folder in case the numbered tag should go astray. Several sheets of the same dried gathering, provided the specimens are neither bulky nor very brittle, can be stored in a single flimsy without damage. They can be finally

tied up in bundles about 3 in. thick, the outer folders being protected by extra sheets of newspaper. The bundles should be tightly packed into cases and liberally sprinkled with powdered naphthalene or paradichlorobenzene. It is essential that the specimens should be completely dry before they are packed in the case; in damp weather mildew quickly spreads from a slightly damp specimen – *Heracleum* is a genus to watch in this respect.

No certificate is required from the British agricultural authorities to import herbarium material into this country – or to export it.

DRYING THE PAPER

Drying the plants ultimately depends on drying the paper used for the daily change. This presents no great problem on a fine day. The paper should be spread out, preferably on a sheltered slope facing the sun. In the Mediterranean summer, paper will dry in ten minutes at 1 p.m., whereas it may take a couple of hours if put out at 7 a.m.; after 4 p.m. it often absorbs moisture instead of losing it. Paper will dry quicker on bare earth or gravel than on grass. Gusts of wind are the chief difficulty. Under these conditions stones should be placed on the paper – a dried-up, gravel river bed, provided a flood does not come down from the hills, is a convenient place. There is a certain kind of Mediterranean *phrygana*, composed of low *Cistus* bushes and the prickly domes of *Poterium spinosum*, that is an ideal community for drying paper on a windy day, particularly if it can be found in the lee of a wood. The paper can be spread over the bushes or propped up between them. Small boys can often be bribed to collect dry paper, but if they are not watched may draw crude pictures on it or make off with it altogether. When staying in towns, the collector should look out for a hotel with a flat roof or large balcony. A ground sheet is useful to spread on the bed while changing the presses.

Our troubles really begin, however, when wet weather prevents us from drying a thousand sheets of paper out of doors. There are various remedies, some of them desperate. I am assuming that radiators or heating cupboards are not available. A small, very simple paraffin stove can be used, and if only a foot or so high can be fairly easily transported. You can put the stove under the hotel bed (having first removed the mattress) and spread out the damp paper on the springs; it will dry in a minute or two. Or you can thread metal "Bulldog" clips on a length of string and suspend them between two chairs above the stove. Several pieces of drying paper can be pushed into each clip, and the convection current rising between the vertical sheets will dry a larger quantity of paper in less time than it takes on the bed. These clips can also be useful for drying sheets in windy weather outside. In a tent a collapsible table with a skeleton top can be used to support presses or paper above the stove.

I have used an iron in Greece, but the process is slow and not to be recommended. The iron puts a patina on the paper and cuts down its power of absorption. My favourite method in Turkey is to find a suitable bakery. Some of the more modest bakeries have a low room above the oven in which wood for the furnace is stored in winter. The floor gets extremely hot, and so does the botanist as he crouches down in the dark, tickled by silverfish that thrive in the inferno, and spreads out his precious paper. It gets beautifully warm and dry, a thickness of 8 or 10 sheets being dried in an hour or so. The drier presses can be put in the bakery overnight, but it is usually too hot for the wetter ones; even with frequent changing the wetter specimens darken perceptibly. Some genera react differently, however. We found that some petaloid Monocotyledons responded well to strong heat; gatherings of *Scilla* and *Ornithogalum* dried in this way made far better specimens than those dried without artificial heat. The oven of a kitchen range, slowly cooling off throughout the night, can also be an effective aid; the presses, however, must be supported on

bricks to raise them off the hot floor of the oven. The charcoal brazier provides a method of drying that does not require liquid fuel, and can prove very useful in a room or tent if one is not overcome by the fumes.

These and other methods must be resorted to if bad weather persists, but in the mountains I always take enough dry paper to last for several days. This may require an extra pack-animal, but is more than worth it in the time it saves. Collecting plants is more enjoyable – and profitable – than crouching over a stove.

ADDENDUM: THE RIGHT FOOTWEAR

Though the object of this article has been the welfare of the collection, it may not be out of place to consider one point in the welfare of the collector. Many an expedition has been interrupted or curtailed by the collector not being suitably shod. More accidents are probably caused by wearing the wrong shoes than from any other cause. Un-nailed walking shoes can be deadly on steep dry grass; boots or shoes studded with nails are often little better on dry rocks. There is a great deal to be said for wearing good mountaineering boots with rubber "Commando" soles – or even gym shoes for short excursions, provided your feet are hardened and your ankles sturdy. Only on wet slimy rocks are nails safer than rubber. If the writer had always taken his own advice and worn rubber-soled boots, he would not have broken his finger, fractured his spine and sustained various wounds that considerably reduced his collecting power.

GENTIANELLA IN BRITAIN

III. GENTIANELLA GERMANICA (WILLD.) BÖRNER

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SUMMARY

Gentianella germanica is taxonomically distinct from British members of the *G. amarella* aggregate, but hybridises freely with *G. amarella* subsp. *amarella*. The investigation of hybrid populations by biometric methods reveals the existence of extensive introgression. Extension of the methods to the examination of apparently pure colonies of both parent species suggests that the range of *G. germanica* was formerly more extensive than it is now, and that it is still dwindling.

ECOLOGY AND DISTRIBUTION

While *G. germanica* occurs in the same general localities as *G. amarella* there is a distinct ecological difference between the two species. *G. germanica* almost always occurs in more sheltered habitats, where the ground is less homogeneously covered with short downland turf. The most frequent situations are in slightly scrubby ground or at woodland margins; and regular associated species are *Agrimonia eupatorium*, *Chamaenerion angustifolium*, *Clinipodium vulgare*, *Crataegus monogyna*, *Festuca* spp., *Fragaria vesca*, *Helictotrichon* spp., *Hypericum hirsutum*, *Rubus fruticosus* agg., *Thelycrania sanguinea* and *Viburnum lantana*.

Colonies of *G. germanica* and *G. amarella* are often found within a few yards of each other. The differences of habitat do not seem to be absolute, and both plants may stray from time to time. Hybrids may occur throughout the range of habitats. They are often found where the ground has been altered by human activities. In the Chilterns, extensive hybrid populations sometimes occur where fields on chalk have been ploughed, sometimes up to woodland margins, or where lanes have been cut through the chalk, and the spoil thrown up in dykes. It is probable that such changes as these are partly responsible for the apparent diminution in the numbers and range of *G. germanica*.

BIOMETRIC WORK

There are many differences between *G. germanica* and *G. amarella*, and the separation of the two species normally presents no difficulty. The chief differences have been summarised by Willdenow (1797) and Wettstein (1896). In Willdenow's original description attention was drawn to the following points.

- (1) Leaves ovate-lanceolate (lanceolate in *G. amarella*).
- (2) Branches longer than the internodes.
- (3) Teeth of the (corolla) fringe ovate, acute.
- (4) Habit different.
- (5) Corolla wider and larger.

(6) Distinctly less yellow root.

Wettstein, in his monograph of the genus, added to or amplified the description thus :

- (7) 5–15 internodes in well-developed plants.
- (8) 2nd or 3rd internode not obviously longer than the rest.
- (9) Branches in the upper (rarely lower) part, but stem usually simple.
- (10) Calyx teeth as long as or slightly longer than the calyx tube.
- (11) Calyx teeth obviously shorter than the corolla tube.
- (12) Sepals not appressed to the corolla, spreading.
- (13) Corolla 15 (in reduced specimens) – 35 mm long.
- (14) Capsule stipitate.

Of these characters, numbers 2, 4 and 9 relate to the habit of the plants. In *G. germanica* the branches are normally restricted to the upper nodes, and frequently form a subcorymbose inflorescence. The pyramidal habit usually found in well-grown plants of *G. amarella* is very rare. The internodes are more or less equal, and in general shorter than at least the lower branches.

In some of the other characters the differences between the two species are not clear. No obvious distinction exists in the shape of the teeth of the corolla fringe, the colour of the roots or the length of the capsule stalks. In both species the stalks of the capsules may be up to 2 mm long. The sepals of fresh *G. germanica* are more spreading than those of *G. amarella*, but the difference tends to disappear in dried material.

The remaining differences can be treated quantitatively. The data obtained when this is done for random samples of the following eight populations of the two species and their hybrids are summarised in Table 1.

		Grid Reference
502 :	<i>G. amarella</i> , Beacon Hill, Oxon.	SU 7599
513 :	<i>G. amarella</i> , E. Woodhay, N. Hants.	SU 4060
514 :	<i>G. amarella</i> , E. Woodhay, N. Hants.	SU 4060
501 :	<i>G. × pamplinii</i> , Crowell Hill, Oxon.	SU 7599
511 :	<i>G. × pamplinii</i> , Ashmansworth, N. Hants.	SU 4157
512 :	<i>G. × pamplinii</i> , Ashmansworth, N. Hants.	SU 4157
504 :	<i>G. germanica</i> , Howe Wood, Oxon.	SU 6991
506 :	<i>G. germanica</i> , Letcombe, Berks.	SU 3784

From the table the following differences between the pure species are most obvious : (for explanation of the indices, see Pritchard, 1959).

(1) *No. of internodes*. Although the range in numbers of internodes overlap (largely owing to the tendency of *G. germanica* to produce slender annual forms) the means are significantly different between 502 (*amarella*) and 504 (*germanica*), the actual difference being 150.

(2) *Leaf shape*. Both leaf indices reveal considerable differences between the species. In leaf L/W the difference between 502 and 506 is 1.21, while in leaf $(B - A)/2L \times 100$ that between 502 and 504 is 4.77.

(3) *Corolla length*. This is the most striking difference between the species. In all specimens of the two examined (not only the random samples) there is very little overlap and such as there is is owing entirely to the slender forms of *G. germanica*, in which all the floral and vegetative organs are reduced in size. The difference between the means of 502 and 506 is 1.22 cms, or 76% of the mean corolla length of *G. amarella*.

(7) *Corolla/calyx ratio*. The calyx in *G. germanica* does not increase in size in proportion to the increase in corolla size. Hence this ratio is very much greater than in *G. amarella*. The actual difference between 502 and 506 is 0.47.

Similar differences are also more or less marked in the other characters shown in the

TABLE 1
Statistical data for *G. amarella*, *G. × pamplinii* and *G. germanica*

Character	<i>G. amarella</i>						<i>G. × pamplinii</i>						<i>G. germanica</i>					
	502		513		514		501		511		512		504		506			
	x	σ	x	σ	x	σ	x	σ	x	σ	x	σ	x	σ	x	σ		
1. No. of internodes	6.41	1.11	5.89	0.95	6.73	1.28	8.07	1.06	6.91	1.53	7.24	1.18	7.63	1.22	8.90	1.51		
2. $(\text{Log } A/T \text{ Int.}) + 1$	1.60	0.40	1.15	0.39	1.61	0.27	1.58	0.52	1.22	0.37	1.36	0.51	1.73	0.49	1.66	0.44		
3. Log Ht./T. ped.	0.89	0.24	0.66	0.33	0.94	0.23	1.03	0.15	0.73	0.25	0.67	0.26	0.82	0.31	0.84	0.20		
4. Leaf L/W	3.11	1.28	3.53	0.77	2.93	0.52	3.43	1.03	2.84	0.87	2.34	0.56	2.13	0.38	2.35	0.65		
5. Leaf $\frac{B-A}{2L} \times 100$	7.95	3.44	5.27	2.77	7.93	3.21	2.39	5.47	4.44	3.49	8.12	3.67	11.38	2.91	9.61	4.35		
6. Corolla length	1.64	0.19	1.63	0.11	1.59	0.13	1.86	0.15	2.41	0.32	2.39	0.46	2.93	0.37	2.83	0.39		
7. Corolla/calyx	1.71	0.23	1.93	0.34	1.75	0.22	1.77	0.25	2.18	0.33	1.07	0.38	2.21	0.23	2.16	0.22		
8. Calyx long/short	1.10	0.13	1.09	0.14	1.15	0.17	1.29	0.33	1.10	0.10	1.06	0.09	1.09	0.10	1.10	0.11		

table, except for the inequality of the calyx. (In general, when all specimens of *G. amarella* and *G. germanica* are considered, the calyx of the latter tends to be markedly less unequal). In each character, the values for the three hybrid populations are intermediate between those of the parents.

TABLE 2
t tests, *G. amarella* and *G. germanica*

Character	Samples	<i>t</i>	<i>p</i>
1. No. of internodes	502, 504	4.18	< 0.001
4. Leaf L/W	502, 506	3.81	< 0.001
5. Leaf $\frac{B-A}{2L} \times 100$	502, 504	4.18	< 0.001
6. Corolla length	502, 506	14.84	< 0.001
7. Corolla/calyx	502, 506	21.20	< 0.001

The results of *t* tests for the four characters above are shown in Table 2. The differences between the two species are highly significant in the samples and characters examined.

An examination of fairly large numbers of herbarium specimens indicated similar differences between the pure species. While the actual ranges of variation were rather greater, the two species remained distinct. Herbarium gatherings of *G. × pamplinii* are usually more or less intermediate in character, although they may range widely between the extremes set by the parent species. In the examination of *G. germanica* and *G. × pamplinii* it soon became apparent that the labelling of specimens did not always agree with their appearance. That is, many specimens of *G. × pamplinii* (recognized by eye) were labelled as *G. germanica*, and to a lesser extent, *vice versa*. Wettstein (1896) points out that backcrosses occur, and this is the impression gained from an investigation of herbarium material. The populations 513, 514, 501, 511 and 512 in Table 1 (all of which are represented by random samples) show a gradual change in general appearance, 513 being most like *G. amarella*. but with some characters of *G. germanica*, while 512 is very like, *G. germanica* but shows traces of *G. amarella* parentage. Wettstein examined the pollen of putative *G. × pamplinii*, and found a high percentage of bad grains (47%). I carried out a further examination for plants from populations 502 (*G. amarella*), 501 and 511 (*G. × pamplinii*) and 506 (*G. germanica*). The results of these investigations (for which details have already been given (Pritchard, 1959) for *G. uliginosa* etc.) are set out in Table 3. These pollen samples are again by no means random but they show a high percentage of good pollen in the parent species, and a much lower and more variable percentage in the hybrids.

Although the hybrids can usually be recognised as such, and some sort of a separation into *F*₁ hybrids and backcrosses made by eye, it seemed desirable to have some method of describing the hybrids more precisely, and thus estimating the extent to which introgression had occurred in various colonies. The results shown in tables 1 and 3 suggest introgression, and this is confirmed by field observations. First, the hybrid populations are by no means uniform, as might be expected if no backcrossing to the parents occurred. Clapham and Timm (1940) have described a situation in which no backcrossing occurs: that between *Juncus articulatus* and *Juncus acutiflorus* in the Oxford area. Here the sterile

TABLE 3
Pollen of *G. x pamplinii*

Population	% good pollen	
	Mean	σ
502 : <i>G. amarella</i> , Beacon Hill, Oxon.	96.0	1.4
501 : <i>G. x pamplinii</i> , Crowell Hill, Oxon.	61.7	5.8
511 : <i>G. x pamplinii</i> , Ashmansworth, N. Hants	53.8	8.5
506 : <i>G. germanica</i> , Letcombe, Berks.	96.0	1.4

hybrid is uniform in its morphological and cytological features. Second, a situation somewhat analogous to that in *Gentianella* is illustrated by *Nuphar x spennerana* and *Saxifraga hirsuta x spathularis*, both of which may occur in situations where one parent is unknown. A rather similar case has been described by Yeo (1956) in *Euphrasia*, where, for example *E. vigursii* (derived from *E. anglica* and *E. micrantha*) occurs in the absence of both parents; though here there is a change in chromosome number, since *E. anglica* is diploid and *E. micrantha* tetraploid. This situation occurs frequently with *G. x pamplinii* (at Crowell Hill, Ashmansworth, etc.), where there appears to be no pure *G. germanica* remaining, although old herbarium specimens indicate that it was abundant in both localities 20–30 years ago. Third, it has been shown in Table 1 that the different populations of hybrids are not alike, varying as they do in the relative prominence of *G. amarella* and *G. germanica* characters.

Various methods of representing introgression were tried. Coded values for characters were summed, as this appeared to have been used with some success by Morton (1956), for hybrid colonies of *Ononis repens* and *O. spinosa*. Pictorial methods were attempted, of the types used by Anderson (1949) in separating introgressed colonies of north American irises. None of these gave a useful separation, although Anderson's methods were rejected mainly because of the dependence of the method on random samples, and the fact that the ranges of variation of the parent species in most cases showed considerable overlap.

A method was required which would give a composite figure for small samples of hybrids, and since for the greatest value this figure should be a linear function, experiments were made with discriminant analysis. This has already been described in some detail, as the method used to separate two taxa within *G. septentrionalis* (Pritchard, 1960). Here the aim is somewhat different: there is no difficulty in separating the parent species, but a function is required to assess the apparent parentage of hybrid plants.

Of the characters available for the analysis, three were eventually selected. These were:

- s*, number of internodes
- e*, leaf L/W
- o*, corolla/calyx ratio.

A trial discriminant analysis was carried out in which a fourth character, *k*, corolla size, was used in place of the corolla/calyx ratio. It was apparent that hybrids could be detected by several features, for example intermediacy in characters *s*, *e*, *k* and *o* above, and that these were not necessarily closely correlated. When corolla size was used in the analysis, it was found that its discriminant value was so high that its effect completely swamped those of the other characters. Thus, a population whose corolla size closely resembled that of *G. amarella* would have a discriminant function approximately equal to that of *G. amarella*, although it might be intermediate in, say, leaf shape. Conversely, a population

resembling *G. amarella* in all respects except corolla size would nevertheless be discriminated as *G. germanica*. Scarcely any separation is gained from the discriminant function beyond that obvious from corolla length alone.

This points out a difficulty and limitation in the use of discriminant analysis. Although the method weights each character according to its numerical values, this weighting is not necessarily related to its taxonomic value. If the numerical differences are too great in one character, then the discriminant analysis will virtually ignore those whose differences are less, but perhaps of equally great taxonomic value. It is necessary to select characters whose apparent numerical values are approximately equal. In this case, although the difference in corolla size between *G. amarella* and *G. germanica* is large and constant, its discriminant value when applied to hybrids is taxonomically little if any greater than that of other characters.

The use of discriminant analysis to analyse hybrid populations, although basically similar to its use for separating distinct, non-hybridising, taxa has certain important differences. Figures 1–3 show the distributions of characters for (a) southern *G. amarella* (populations 502 and 515 combined); (b) hybrids (populations 501, 511 and 512); (c) *G. germanica* (populations 504 and 506), and (d) a combination of (a), (b) and (c). The characters shown are (s) no. of internodes, (o) corolla/calyx ratio and (e) leaf L/W.

From these histograms it can be seen that the frequency distributions of characters for *G. amarella* and *G. germanica* are distinct, whereas those for the hybrids are intermediate.

When the frequency distributions are combined (Figs. 1 (d), 2 (d), 3 (d)) curves

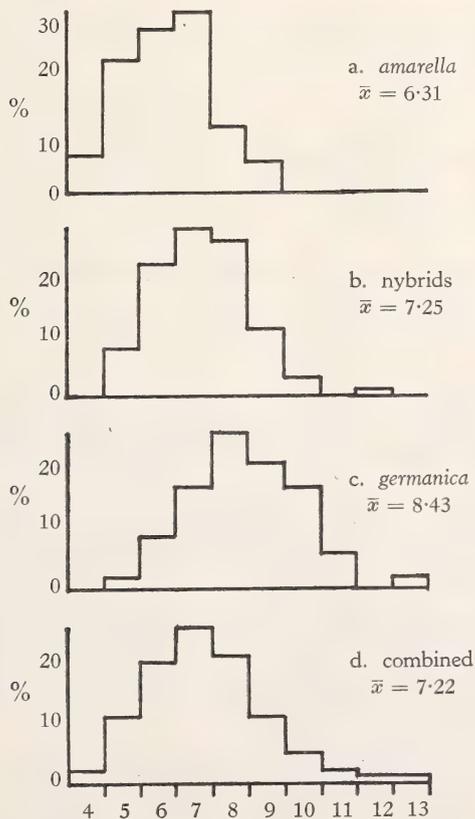


Fig. 1. Number of internodes in *G. amarella*, *G. germanica*, and hybrids.

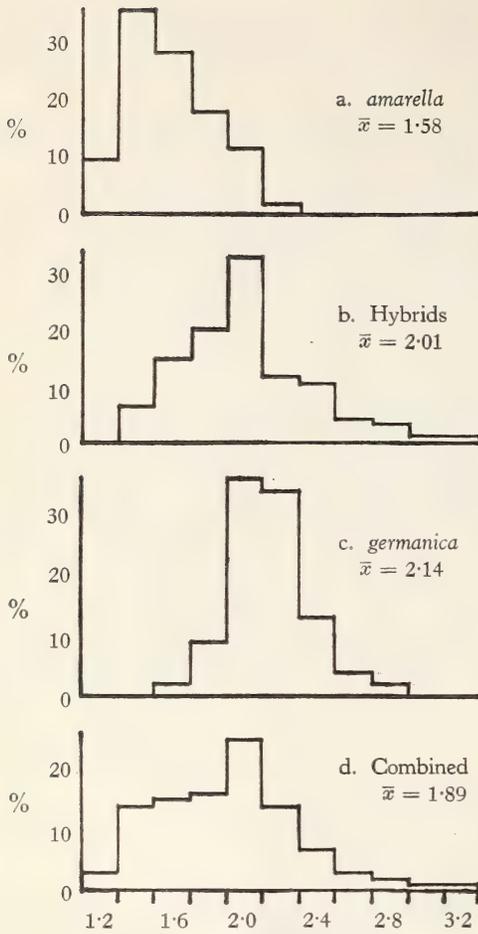


Fig. 2. Corolla/calyx ratio.

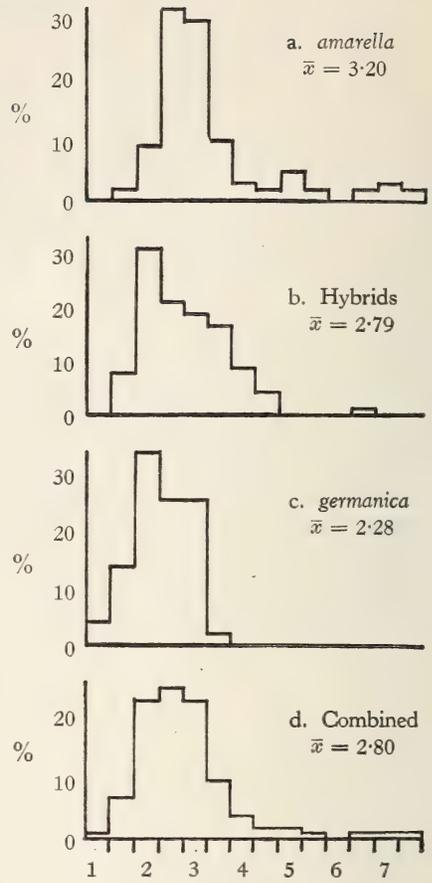


Fig. 3. Leaf length/width.

are obtained which are approximately unimodal. This indicates that, taken together, the two parent species and their hybrids form a large population with its variation about a single mode. The same conclusion is suggested when all herbarium specimens are treated similarly.

The calculation of the discriminant function requires the establishment *a priori* of a number of primary groups. In the first place, these primary groups were taken as the parent species, and no account was taken of the hybrids in the calculation. The discriminant functions of the hybrids could then be derived from the coded values of characters for each plant and the weighting factors obtained from the parent species. This method gave a reasonably satisfactory distribution of the discriminant functions for the hybrids. It was however, subsequently suggested (Finney, personal communication) that a better separation might be obtained by using recognisable groups of the hybrids as some of the primary groups, and this proved to be the case. The calculation of the weighting factors is the same as in the case of *G. septentrionalis* (Pritchard, 1960). The weighting factors eventually obtained are shown in Table 4.

TABLE 4. Weighting factors

No. of internodes	+ 2.4859	\cong + 2.5
Corolla/calyx ratio	+ 3.0296	\cong + 3.0
Leaf L/W	- 1.0000	$=$ - 1.0

The mean values of the discriminant function for each of the random samples, together with certain combinations of these, are shown in Table 5. The order of the samples within the table is that of their apparent parentage judged by eye. With the exceptions of the two pairs of samples from East Woodhay and Ashmansworth this is also the order of their discriminant functions.

(1) The mean value for 502 and 515 is 116.5, rather less than that for A1 – A106 (129.9). These are colonies of apparently pure *G. amarella*, and this value may be taken as that for southern *G. amarella* as a whole.

(2) When the total includes 513 and 514, the mean rises to 129.9, the combined mean of these two samples being 150.4. During work on *G. amarella* (Pritchard, 1959) it was felt that certain chalk populations, these two included, showed divergences from the majority. These divergences are all of the sort evident in 513 and 514. They indicate a degree of introgression from *G. germanica*, which is abundant in the area, although not now found in the immediate vicinity of populations 513 and 514.

TABLE 5
Mean values of F for random samples of *G. amarella*, *G. germanica* and hybrids

Nos.	Population	Mean value of F
A1-31	502 : Beacon Hill (23)	116.3
A74-106	515 : Abinger (17)	116.7
A32-56	513 : E. Woodhay (12)	154.0
A57-73	514 : E. Woodhay (12)	145.0
P58-72	501 : Crowell (23)	176.3
P26-57	511 : Ashmansworth (12)	223.7
P1-25	512 : Ashmansworth (12)	222.9
G1-16	504 : Howe Wood (23)	256.9
G17-47	506 : Letcombe (22)	276.0

(3) 501 resembles *G. amarella* in a general way although several characters suggest introgression from *G. germanica*. The latter species was formerly plentiful in the same locality. This is in good agreement with the sample's discriminant function of 176.3 which is closer to *G. amarella* than to *G. germanica*, being below the calculated mid-point of 196.4.

(4) The field inspection suggested that 511 and 512 contained a large proportion of F_1 hybrids. The theoretical F for F_1 hybrids should be 196.4, the calculated mid-point, but the value for 511 and 512 of 223.3 is rather above this.

(5) Between 504 and 506 certain differences have been noted, such as the lower number of internodes in 504. The values of F (256.9 and 276.0) again suggest introgression from *G. amarella* in 504, which agrees with field observations. Owing to the presence of *G. amarella* only about 50 yards from the Letcombe colony, it may well be that the value for pure *G. germanica* would be even higher than 276.0.

Thus the discriminant function provides a reliable guide to the parentage of random samples of hybrid populations, confirming field observations and impressions. Figure 4 shows the distribution of F for the random samples. 502 and 515 are treated as *G. amarella*, 513 and 514 as "amarelloid" hybrids, 501, 511 and 512 as hybrid colonies containing

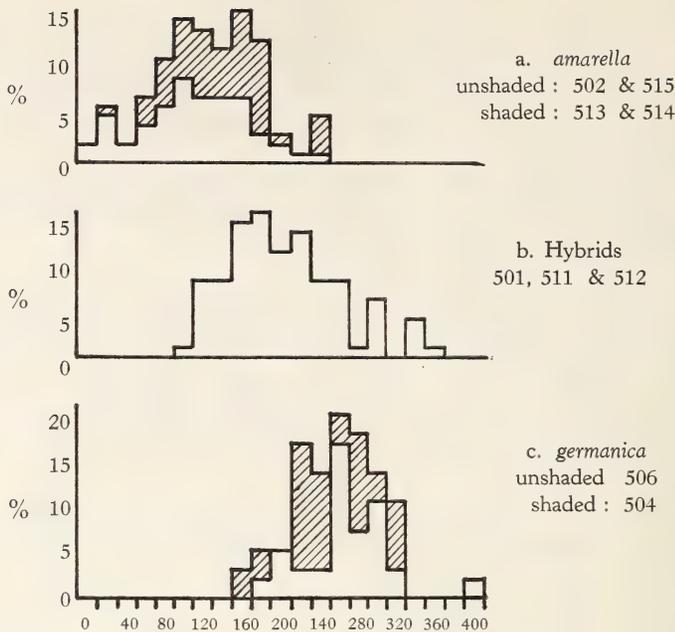


Fig. 4. Distribution of F for random samples of *G. amarella*, hybrids, and *G. germanica*.

more or less of each parent and 504 and 506 as *G. germanica*, 504 showing slight introgression from *G. amarella*. From the histogram it is clear that a good separation is obtained. The actual overlap between pure *G. amarella* and pure *G. germanica* is only 19%. If 513, 514 and 504 are included, the overlap rises to 40%. The hybrids occupy an almost exactly intermediate position.

In 504 and 506 the mean F falls just outside the overlap. In 502, 513, 514 and 515 it is well outside. (The values for 506 alone and for 502 and 515 are of course further away). Coupled with the shape of the histograms, these figures suggest that in the plants so far considered, "pure" *G. amarella* (i.e. 502 and 515) is "purer" than "pure" *G. germanica* (i.e. 506). This is borne out by examinations of herbarium material; traces of introgression can often be seen in *G. germanica*, but rarely in *G. amarella*. This is partly owing to the tendency of botanists to separate hybrids (as *G. × pamplinii*) from *G. amarella* more readily than from *G. germanica*. For example, a larger corolla and ovate-lanceolate leaves are more striking in a population of *G. amarella* than are a smaller corolla and lanceolate leaves in one of *G. germanica*. Further, the geographical range of *G. germanica* in Britain lies entirely within that of *G. amarella*, which is very much wider.

An analysis of herbarium material reveals several interesting points. In Table 6 plants from southern chalk and limestone localities are split into four groups :

- (a) Plants from known *G. germanica* areas.
- (b) Plants from chalk areas where *G. germanica* does not grow (excluding (c) below).
- (c) Plants from Surrey, Kent and East Sussex.
- (d) Plants from oolite localities.

Group (d) has the lowest value, which is similar to that for the random samples of *G. amarella* (117). Group (b) comes next, and its mean value is not significantly different ($p > 0.05$) from that of pure *G. amarella*. Group (a) has the highest value, slightly higher than that of the Crowell hybrids (501 : mean F = 176). There is a tendency for

TABLE 6

Group	Range of F	Mean F
(a)	75-251	179
(b)	21-226	135
(c)	56-256	157
(d)	69-169	115

collectors to gather large and striking plants for their herbaria, and these are just those which are most likely to show introgression from *G. germanica*. It must be concluded that introgression is widespread in the areas in which the two species occur together.

Group (c) was separated from Group (b) because the plants showed some of the characters of *G. germanica* in small measure. The mean F for these plants is considerably higher than that of group (b) and approaches that of group (a). There are two possible inferences from these data. There may be local variation in *G. amarella* in S.E. England, which does not seem unlikely. However, no such variation appears to occur elsewhere within the range of the chalk and southern limestone race of *G. amarella*. Alternatively, the data may indicate earlier introgression from *G. germanica*. Although apparently suitable habitats abound in Surrey, Kent and Sussex for this species, similar to those in which it is found in the Chilterns, it does not now occur in Britain east of Hertfordshire, Buckinghamshire and Berkshire. Many plants placed by Matthews (1955) in the Continental element of the British flora (e.g. *Cirsium acaule*, *Ophrys insectifera*) occur with *G. germanica* in its present habitats and also extend along the North and South Downs. In view of the European distribution of *G. germanica* (mountains of central, north and east central Europe) it is surprising that it does not occur in S.E. England. Further, it has been shown that in some localities where undoubted hybrids are found, and whence *G. germanica* has in the past been recorded, it no longer occurs. It seems probable that this species did once occur on the Downs, and that over a long period introgression with *G. amarella* has obliterated all but traces of it. (Cf. *G. uliginosa* in South Wales (Pritchard, 1959)).

Tables 7 and 8 show the means of F for a number of small herbarium samples of *G. germanica* and *G. × pamplinii*, grouped according to the herbarium labelling. The column headed "appearance" is my own estimation of the sample's parentage.

Of the samples labelled *G. germanica*, all except four (657-61, 72-4, 102-4 and 105) appear more or less pure, while three (G 85-9, 119 and 137-8) are nibbled and show low values of F. The mean value for all these samples, excluding those seven but including P 81-82 (labelled *G. × pamplinii*) is 279, very slightly higher than that of sample 506 (276). *G. amarella* is not a common plant in those parts of Buckinghamshire (the Chiltern scarp) where *G. germanica* is abundant, primarily owing to the scarcity of open grassland free of scrub. It is therefore of some interest that the mean value for Buckinghamshire plants is 314, rather higher than that for the plants as a whole. After removal of the Buckinghamshire plants the mean of the rest is 262. For those localities in which I know that *G. amarella* also occurs, the mean value is 256 (plants from Crowell, Letcombe, Ashmansworth, Waterslip, Chinnor, Shelbourne and Assenton).

Among plants of *G. × pamplinii* (G 57-61, 72-4, 105, P 73-80, 83-117) the mean value is 207. Only six samples differ from the mean by more than 20 points. Of these, P 92-4 and 114-5 are apparent backcrosses (*G. germanica* × *G. × pamplinii*) while P 85-6 and 116 are slender annual forms. If these are omitted, the mean value for *G. × pamplinii* is 204.

TABLE 7
Specimens labelled *G. germanica*

Nos.	Date	Appearance	Mean F
G 48-50	1820	G	288
51- 4	1879	G	339
55- 6	1898	G	307
57-61	1897	AG	211
62-71	1883	G	255
72- 4	1892	AG	220
75- 6	1903	G	273
77	1915	G	298
78-80	1923	G	289
81- 2	1923	G	325
83- 4	1895	G	204
85- 9	1927	G (nibbled)	248
90- 2	1890	G	266
93-101	1892	G	229
102- 4	1883	aG	264
105	1917	AG	227
106- 8	1878	G	300
109-11	1904	G	384
112- 8	1913	G	296
119	1921	G (nibbled)	157
120- 5	1910	G	227
126	1913	G	295
127	1913	G	297
128-30	1930	G	241
131- 5	1931	G	339
136	1941	G	272
137- 8	1941	G (nibbled)	147
139-41	1941	G	309
142- 4	1942	G	302
145-52	1894	G	246
153- 5	1937	G	306
156- 7	1864	G	303

Appearance : G = *G. germanica*
aG = hybrids resembling *G. germanica*
AG = more or less intermediate

While these samples are neither random nor, probably, uninfluenced by collectors' bias, after the above corrections the following relationship emerges :

- (a) Mean F for 'corrected' *G. amarella* (random samples 502 and 515) = 117
(b) Mean F for 'corrected' *G. × pamplinii* (as above) = 204
(c) Mean F for 'corrected' *G. germanica* (Buckinghamshire plants) = 314

The average of (a) and (c) is 216, and if (a) and (c) represent pure species, this would be the expected value for (b). The actual value is not much lower than this.

It seems that pure *G. amarella* colonies are easiest to find, largely owing to the much wider range of this species. Pure *G. germanica* is much more elusive, and probably the best remaining localities are those on the scrubby slopes of the Thames Valley in Bucks. Throughout the rest of the range of *G. germanica*, *G. amarella* also occurs, and is usually the commoner species. The two species hybridise freely, and the F₁ is quite fertile, with the result that hybrid swarms occur and introgression is marked. In some places (Crowell

TABLE 8
Specimens labelled *G. × pamplinii*

Nos.	Date	Appearance	F
P 73-80	1946	AG	210
81- 2	1917	G	259
83- 4	1892	AG	207
85- 6	1892	AG	155
87	1895	AG	214
88-91	1913	AG	204
92- 4	1913	aG	261
95- 8	1915	AG	187
99-109	1910	AG	186
111- 3	1921	AG	236
114- 5	1897	aG	282
116	1915	AG	115
117	1889	AG	213

Hill, East Woodhay, Kent) this has proceeded so far that *G. germanica* can no longer be found, but the remaining *G. amarella* shows distinct traces of past introgression. A new use of the method of discriminant analysis has rendered the analysis of such populations less subjective, and confirms observations made in the field.

TAXONOMY

GENTIANELLA GERMANICA (Willd.) Börner (1912); *Gentiana germanica* Willd. (1797); *Gentiana Amarella* var. α Froelich (1796); *Gentiana Wettsteinii* Murb. (1892).

Linnaeus (1753) did not distinguish between *G. amarella* and *G. germanica*, though it has earlier been remarked that there are specimens of both species in Linnaeus' Herbarium (Pritchard 1959). Froelich (1796) amplified Linnaeus' description in such a way as to suggest that it referred to *G. germanica*, though he gave six varieties. Froelich's description of the type follows in part (translated):

"Stem . . . faintly hexagonal, purplish, with branches in the leaf axils. . . .

Cauline leaves sessile, very slightly connate, ovate or ovate-lanceolate, acute or sub-acute; the uppermost ones subcordate, acute. Flowers an inch long.

. . . . Corolla purplish-blue five-toothed, with ovate-lanceolate teeth about of the corolla-tube in length."

In this description the distinctive characters of *G. germanica* are listed, and in his original publication of the name Willdenow (1797) includes as a synonym of *G. germanica* Froelich's *G. Amarella* excluding varieties.

Froelich did however, use the name *germanica* for his varieties β and α of *G. campestris*. For this reason Murbeck (1892) published the name *G. Wettsteinii* to replace *G. germanica* Willd., and this change was retained by Wettstein (1896). Since Froelich used the epithet only for a variety, Willdenow's name is correct.

The British specimens of *G. germanica* are indistinguishable from the Continental plants. No specimens seen by Willdenow, or his type, have been seen, but a number of the exsiccata cited by Wettstein and plants seen by him have been examined. These are: (cited) *Reliquiae Mailleanae* no. 862, *Herb. d. Fl. loc. d. Fr.* no. 68, and (labelled

"Revidit R. v. Wettstein"), Dörfler *Herb. Norm.* nos. 3755 and 3756. There is no confusion about the identity of the British plant, and no change is proposed in the status of the species.

Geographical Distribution

Wettstein gives the Continental distribution of *G. germanica* as : Sweden, England (Harefield and Letcombe Castle), north and east France, Belgium, Germany, Austria-Hungary, Switzerland.

In Britain, the plant is restricted to the chalk of south-east England. I have seen specimens from the following vice-counties : 7, 12, 20-24, 30.

Druce (1932) gives in addition the following vice-comital records for *G. germanica* : 5, 8, 17, 19, 45, 51, 57. Of these, 5 seems scarcely likely as it is completely away from the chalk, but the possibility must be borne in mind. 17 in particular is quite possible. 19 again is possible, but 45, 51 and 57 seem improbable.

No trace of the record for v.c. 57 can be found. That for vice-county 51 was made by Dallman (1908) for "The Marian, Cwm," and for "Limestone common skirting the road East of Glol, alt. 700'." No further records nor specimens have been traced from either of these localities. The Tenby record (v.c. 45) was made by Falconer (1848). Hyde (personal communication) considers the record probably mistaken, as no sign of the plant has been seen since.

GENTIANELLA × *PAMPLINII* (Druce) E. F. Warb. (1952) = *G. amarella* × *G. germanica*; *Gentiana* × *Pamplinii* Druce (1893); *G. axillaris* × *G. Wettsteinii* (Wettstein 1896).

In 1893 Druce described what he believed to be a hybrid, *G. amarella* × *germanica* = *G. × pamplinii*, from Letcombe Castle in Berkshire. He remarked that in the locality a good deal of *G. amarella* continued in flower with *G. germanica* (this is probably largely due to introgression; there is normally only a slight overlap between the two species). He stated that the obconical corolla tube of *G. germanica* fully distinguished it from the nearly cylindrical tube of *G. amarella*, and that the hybrid was certainly somewhat intermediate in character. The specimen was sent to Wettstein, who described in it 1896. Druce (1896), having by then had a reply from Wettstein, further described the hybrid thus. "(The plants) had a longer and more conspicuous corolla than *G. Amarella*. The corolla was more cylindrical than that of *G. germanica*, and the tint was nearer the dark purple of *Amarella* than the bluish purple of *germanica*. The pollen was defective, and the plant was in my opinion distinctly a hybrid of the two species with which it occurred,"

The specimen is in the Druce Herbarium at Oxford, labelled "*Gentiana Amarella* × *germanica*, Letcombe Castle, Berks., Sept. 1892. G. C. Druce and B. Taylor." It is also labelled on the sheet "Type Spec." in Druce's handwriting.

The distribution of those plants I have seen is v.c.'s 7, 12, 22-24.

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BOOK REVIEWS

Darwin's Biological Work, Some Aspects Reconsidered. P. R. Bell, J. Challinor, J. B. S. Haldane, P. Marler, H. L. K. Whitehouse, J. S. Wilkie. Edited by P. R. Bell. Pp. xiii+343, with six plates and 49 text figures. Cambridge University Press, 1959. Price £2.

The centenary of the publication of *The Origin of Species* has focussed attention again on this, the major aspect of Darwin's work. It has also resulted in the publication of various books about Darwin, and yet another can be justified only if it is of outstanding merit. This collection of essays is an attempt to show the diversity of Darwin's interests, and the result is rather uneven. To write a review of 100 years' work for the intelligent layman as well as the scientist is a task that few can measure up to, and not all the contributors have succeeded. However, I read this volume with considerable enjoyment, and think it should be present in any biological library.

Of the six essays, one is of particular interest to readers of *Watsonia*; that on cross and self-fertilization in plants. Before dealing with this a few comments on the rest would be apposite.

Bell's review of the development of work on tropisms in the last hundred years serves to show how original Darwin's ideas were in this field, and also how much has been achieved since. Challinor's discussion of palaeontology emphasises that many of the gaps that Darwin found in the fossil record have not yet been filled satisfactorily. Wilkie, in his discussion of the work and ideas of two of Darwin's distinguished predecessors, Buffon and Lamarck, brings out once more the fact that Darwin was really the great synthesizer who presented in a truly original way the ideas that had been fermenting in men's minds for decades.

J. B. S. Haldane contributes an excellent brief sketch of natural selection. It does illustrate the difficulty of trying to suit two types of reader, however. He includes a 'sketch of Genetics' that is too brief to help the layman and superfluous for the trained biologist. Incidentally, the primrose is referred to as *P. veris* in this paper!

Perhaps the most successful contribution, in the sense that it should be easily understood by the non-scientist, while at the same time it will hold the interest of the biologist, is Marler's review of the progress made in the study of animal communication since the publication of *The Expression of the Emotions in Man and Animals*.

It is unfortunate that the discussion of cross and self-fertilization in plants is in some ways the least satisfactory in the book. There are serious omissions of recent work; one gets the impression that the author has not consulted much literature since 1956, and since the volume was published in November 1959 this cannot be due to the publisher's deadline.

On p. 241 the difference in site of pollen inhibition in two groups is discussed. In the *Parthenium-Crepis* type inhibition is on the stigma; in the *Nicotiana-Veronica* type it is during growth down the style. No reference is made to Brewbaker's (1957) discovery that the site of inhibition can be correlated with the time of division of the germinative nucleus in the pollen grain. Plants with the *Crepis-Parthenium* system show inhibition before germination of the pollen on the stigma and have tri-nucleate grains, whereas plants with the *Nicotiana-Veronica* system generally produce longer pollen tubes in incompatible crosses and have binucleate pollen grains. Brewbaker suggests that the site of inhibition may be related to the level of metabolic reserves in the pollen grain.

Homostyly is mentioned (p. 242) without any reference to Dowrick's (1956) work on *Primula obconica* in which she discussed the production and behaviour of homostyles in detail.

Incompatibility in the Hymenomycetes is discussed without mention of Raper's (1958) discovery that the two incompatibility genes A and B in *Schizophyllum commune* each comprise two loci and that crossing over within the "A" pair can produce incompatible reactions, which are, furthermore, the same as some naturally occurring mating types. A new discovery of this importance deserves mention in a critical review.

It is stated that the commonest cause of the death of the young embryo in interspecific crosses is "a lack of harmony between the embryo and endosperm." This view has been put forward in the past but it is by no means established that this is the case.

If Muntzing's suggestion that perennials may have evolved from annuals because perennial species often have double or higher multiples of the chromosome numbers of related annuals is quoted, surely it should be pointed out also that more recently Stebbins has put forward the view that the presence of vegetative reproduction and the perennial habit in diploid organisms makes them more likely to develop polyploidy. Plants with such characteristics can pass through the "bottleneck of sterility" which may ensue after the onset of polyploidy.

In addition to these and other omissions, the quality of the photographs in Plate V is inexcusable, some

are barely in focus, and in addition they are incorrectly labelled. The legends to photographs i and ii are transposed, and the flowers in photograph vi are in the reverse position to that stated.

The book has one final infuriating feature (to this reader). This is the method of listing references by number at the end of the book, and referring to them in the text by a small index number, often without even stating who the author is. If space saving is the aim, it must be negligible in a volume of this size. If this method is thought to be convenient, then it is a failure. There is no index.

S. R. J. WOODELL

Excursion Flora of the British Isles. A. R. Clapham, T. G. Tutin and E. F. Warburg. Cambridge University Press, 1959. Price 22s. 6d.

Although the publication of Clapham, Tutin & Warburg's *Flora of the British Isles* has been one of the landmarks of postwar British botany, the need has long been felt in this country for a more concise Flora which could be accommodated in the average sized pocket. This has been admirably met by the work under review which bears the title of an *Excursion Flora*.

The problem in writing an *Excursion Flora* is largely one of selection – for many features have to be omitted or modified so as to bring the text down to manageable proportions. Fortunately the number of species involved in the British flora is sufficiently small to have allowed a spacious format, closely resembling that of the larger *Flora*. As the authors note in the foreword, space has been saved by restricting the number of species described in detail (mainly to those common in lowland parts of the British Isles), by the shortening of the descriptions, and by the omission of such features as pollination mechanisms, life forms, chromosome numbers and extra-British distribution. Species not described are, however, included in the keys. The result does not much resemble the more traditional *Excursion Flora* where brevity is usually achieved by cutting out or abbreviating generic descriptions, the combination of species keys and descriptions in some way or other, and a liberal use of abbreviations. The authors rightly stress, however, the importance of adequate descriptions as part of taxonomic practice, a point which raises the question of the public at which the *Flora* is aimed. Certainly Universities have been set a problem by the availability of both the larger and the *Excursion Flora* for their students. I imagine that many will have made possession of the *Excursion Flora* a minimum requirement while recommending the larger *Flora* as a necessity for advanced students.

For the professional or dedicated amateur botanist possession of both *Floras* is desirable since the *Excursion Flora* is in many ways more up to date, including recent additions to the British *Flora* and incorporating many taxonomic alterations (at both generic and specific level) and nomenclatural changes. Here a few criticisms may be levelled against the authors: since many users will wish to correlate the two *Floras* it is unfortunate that more care has not been taken to facilitate this. Thus, for example, *Dactylorhiza* is separated from *Orchis* in the new *Flora* but there is nothing to indicate that *Dactylorhiza incarnata* is the same as *Orchis strictifolia* of the larger *Flora*. No synonyms are given in this case and the index lists only *Orchis (Dactylorhiza)*. Yet in other cases where the specific epithet is retained unchanged, the synonym is given in both the text and the index, e.g. *Anchusa arvensis* (L.) M. Bieb. (*Lycopsis arvensis* L.).

Some species such as *Cochlearia micacea* have disappeared without trace; other species have been remodelled, such as *Calystegia sepium*. We must look forward to the next edition of the larger *Flora* or to separate publications for the explanation of the various alterations made.

Species aggregates are used occasionally but in some cases the aggregate is numbered as though it were a species and the component species unnumbered (e.g. *Dryopteris filix-mas* agg.). In other cases, e.g. *Dactylorhiza maculata* agg., the component segregates are (correctly) numbered. In *Alchemilla* the *vulgaris* aggregate is indicated in the key but the species are numbered normally. In the case of *Polypodium vulgare* L. we are told that it is an aggregate containing three British species, distinct morphologically and cytologically, without details. *Euphrasia officinalis* L. is given as *sensu lato*, and noted as divisible into other species. These are small points in themselves but a more consistent usage in the case of aggregates would cause less confusion.

Misprints and minor inconsistencies (such as both Bieb. and M. Bieb. as abbreviations) are few. A major lapse is the omission of the *Gentianaceae* from the family key.

While the printing does not conform to the highest standards of the Cambridge Press, the type and paper are excellent and the imitation buckram binding very serviceable. At a price of 22s. 6d. the book is remarkably good value.

V. H. HEYWOOD

The Making of the Broads : a reconsideration of their origin in the light of new evidence. J. M. Lambert, J. N. Jennings, C. T. Smith, C. Green and J. N. Hutchinson. Preface by H. Godwin. Pp. 153, with 7 half-tone plates and 63 maps and diagrams. R.G.S. Research Series, No. 3. 1960. Royal Geographical Society and John Murray. 25s. 0d. Available from the Royal Geographical Society, 1 Kensington Gore, London, S.W.7 at 26s. 2d. including postage.

This book records the evidence for one of the most unexpected recent discoveries concerning the history of British vegetation : that the Norfolk Broads are Man-made features, dug out by hand in Medieval times. In the past it has generally been assumed that the Broads had a natural origin; and in fact an hypothesis for a natural origin of the Broads was put forward, with some misgivings, by two of the present authors as recently as 1951. In the course of their work, they found certain features that were difficult to explain if the Broads had indeed evolved naturally. Subsequent more numerous and more closely-spaced borings showed everywhere that the Broads occupy steep-sided and more or less flat-bottomed basins in the surrounding valley peats, in some cases with straight steep-sided balks of the same peat standing above the general level of the floor of the basin. It became clear that the Broads could scarcely be accounted for except as a vast series of artificial peat-cuttings. The presentation of the massive stratigraphical evidence obtained by Dr. Lambert and Dr. Jennings occupies almost half the book. Some idea of the scale of the work is given by the fact that the stratigraphical results are based on some 2,150 borings, distributed throughout the Broadland valleys.

In part II, C. T. Smith sets out extensive contemporary evidence for medieval peat digging in the Broads, vividly corroborating Lambert and Jennings' stratigraphical conclusions. The earliest records of turbarry are from the mid-twelfth century. For the next two centuries there is abundant evidence of a flourishing turf industry in all the main areas where Broads exist at the present day. In the latter half of the fourteenth century a change in the words used to describe areas which were formerly turbarry suggests that these were becoming wetter; and at the same period there is evidence of decline in the sales of peat, and of increasing difficulty in its extraction. By the fifteenth century peat was being won in few places, and there by dredging; and the documents suggest that the turbarries had largely given place to open water and fen. Rough calculations show that, given several centuries for the work, the digging out of the Broads by hand is within the bounds of practical feasibility.

In part III, C. Green and J. N. Hutchinson give an account of archaeological and stratigraphical investigations which impinge on the theme of the first two parts. They show that after the Romano-British marine transgression Broadland was first densely populated by Danish settlers at the end of the ninth century; and that in late Saxon and early Norman times the area stood some 13 feet higher relative to sea level than now : submergence has been a gradual and progressive process from about the time of the Norman Conquest to the present day.

The diverse specialities of the authors, and the variety of their evidence, are symptomatic of the way in which the conclusions of peat stratigraphy and vegetational history interweave with those of ecology, geography, archaeology, history, and other kindred subjects. The inevitability with which the diverse lines of evidence converge on the main conclusions makes this book a fascinating and very satisfying example of scientific investigation and exposition. It will give food for thought to all who are interested in the Broads, botanically or otherwise; and it provokes respect for our forbears whose spades moved some nine hundred million cubic feet of peat and gave us an attractive and interesting addition to the diversity of our country.

M. C. F. PROCTOR

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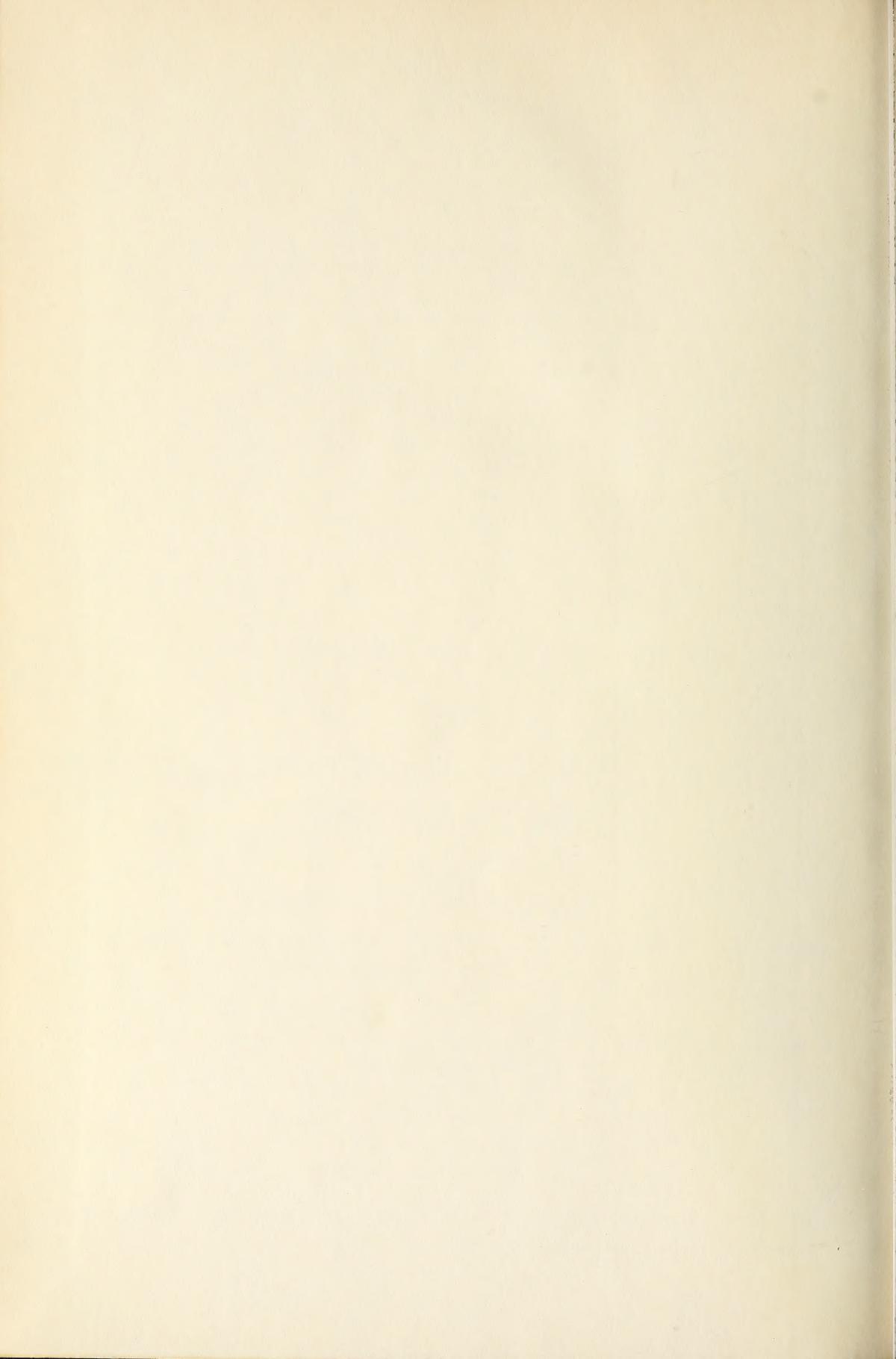
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