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* (Pugsl.) 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 spathulate, 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 (Pugsl.) 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 spathulate 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	
	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	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 $> 0{\cdot}05$
3 stops : ,, $< 0{\cdot}05$
4 stops : ,, $< 0{\cdot}01$
5 stops : ,, $< 0{\cdot}001$

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	$5.\frac{1}{3}.4.2. \ldots 6$
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 $p > 0{\cdot}05$)
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 $p = 0{\cdot}05$ level, it differs significantly from all other groups except Group 3. Its coefficient of variation ($C_V = 16{\cdot}2\%$) is the least of all groups : (e.g. in group 3 $C_V = 17{\cdot}5\%$, while in the homogeneous group 1 $C_V = 18{\cdot}8\%$). (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.

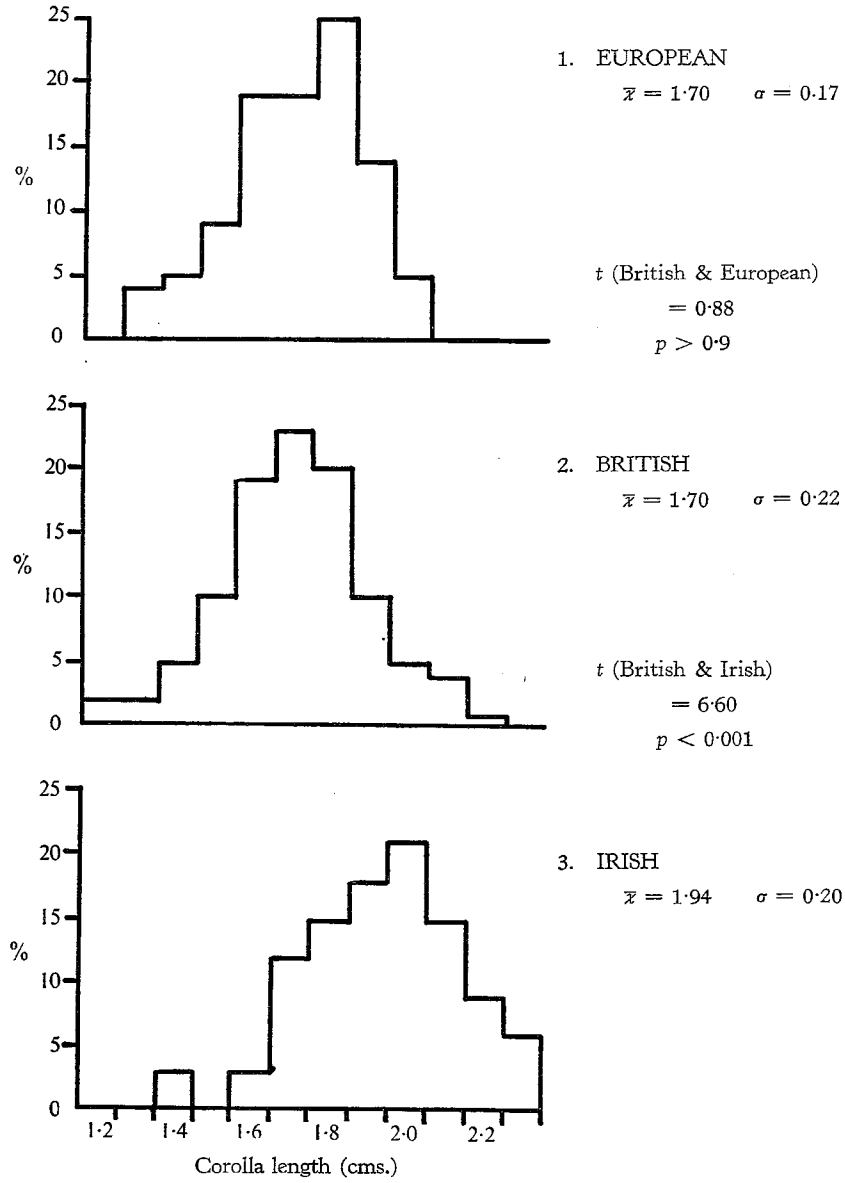


Fig. 1. Corolla lengths of British, Irish and European *G. amarella*.

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 $\left(C_V = \frac{100 \times \text{standard dev.}}{\text{mean}}\right)$, 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.) Wetts. (1896).

According to both Wettstein and Murbeck, *G. lingulata* is represented in Britain only by var. *praecox* (Towns.) Wettst. This variety (= *Gentianella anglica* (Pugsl.) E.F. Warb.) is discussed later. The common British plant (according to Wettstein) is *Gentiana axillaris* (Schmidt) Rchb.

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 ± equal, or else the terminal one reduced to about 1 mm. Basal leaves of first year lanceolate to lingulate, of second year obovate or spathulate. Stem leaves lanceolate to ovate-lanceolate, ± 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, ± 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 corrolla-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.

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	*G. amarella*				*G. anglica*						*G. lingulata*	
	Oxon.		*Surrey*		*Surrey*		*Lincs.*		*Berks.*		*Europe*	
	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	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 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*		*lingulata*	
	$\bar{x}$	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 spathulate.

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 (Pugsl.) 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 (Pugsl.) E. F. Warb. subsp. *anglica*.

Plant 4-20 cm. high, of 2-3 (- 4) internodes. Terminal internode about 1½ times as long as the average, occasionally contracted, when the second one is much expanded. Terminal pedicel forming about ½ the height of the plant, frequently even more. Basal leaves narrowly spathulate, 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 1½ 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 ⅓ of the height of the plant. Basal leaves broadly spathulate 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 1½ 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 spathulata 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 1½-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*

	amarella group 1		*amarella* group 2		438		518		519		*Continental uliginosa*	
Character	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	$\bar{1}$·79	0·41	$\bar{1}$·72	0·47	$\bar{1}$·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 spathulate. 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	*amarella*			519A		
	Range	x	σ	*Range*	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			*uliginosa*		
	Range	x	σ	*Range*	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.

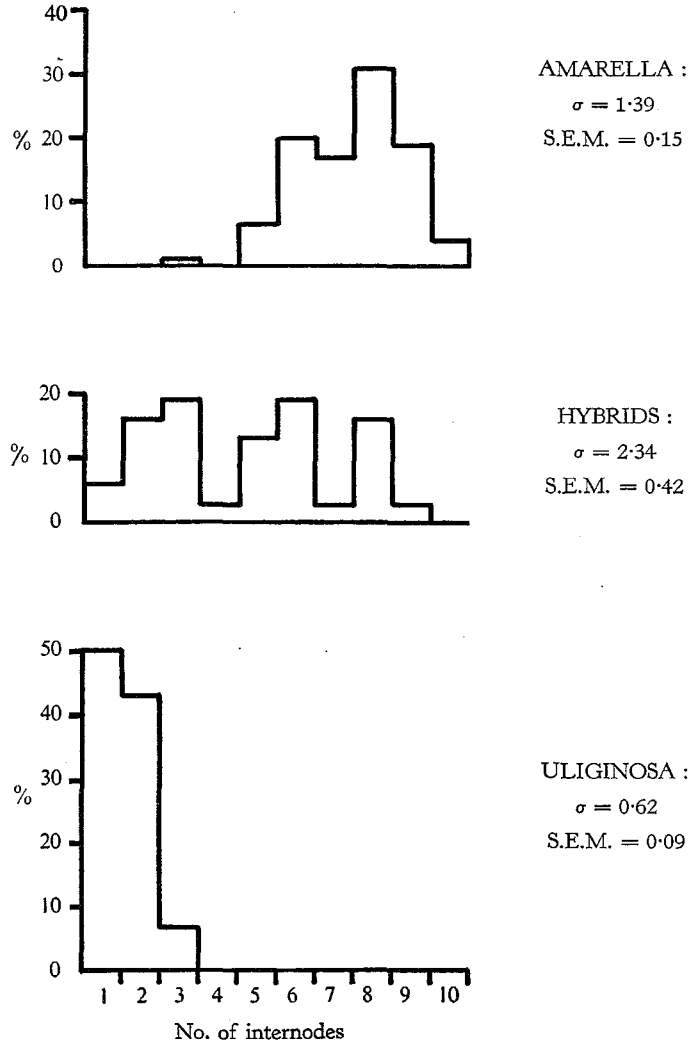


Fig. 2. *G. amarella*, *G. uliginosa* and hybrids : no. of internodes.

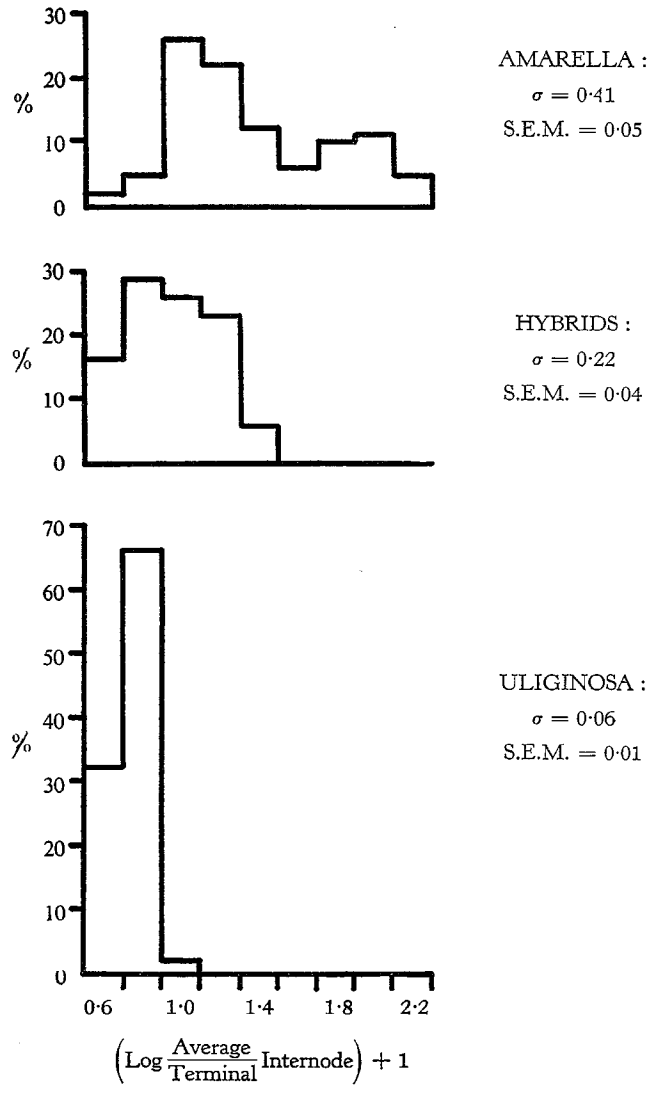


Fig. 3. *G. amarella, G. uliginosa* and hybrids : relation between terminal and average internode lengths.

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*
*a*marella :	521; Kenfig, Glamorgan	95·0 ± 06·7
Hybrids :	519a; Oxwich Burrows	70·0 ± 12·7
*u*liginosa :	438; Oxwich Burrows	89·0 ± 07·0

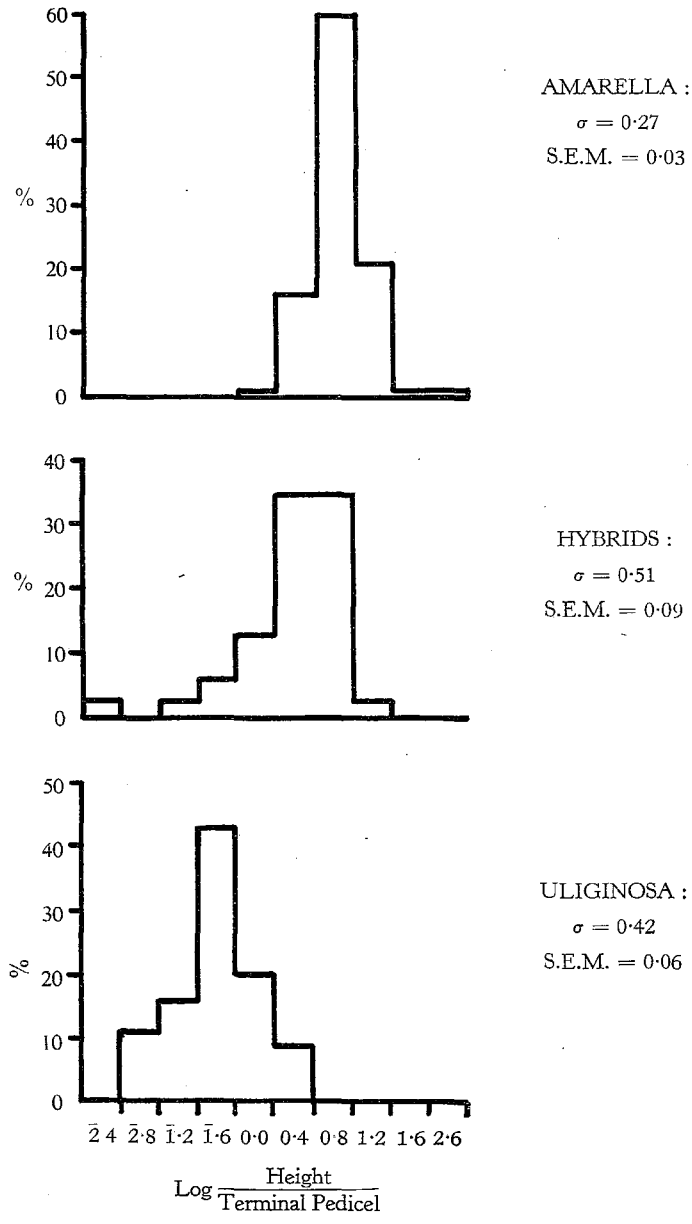
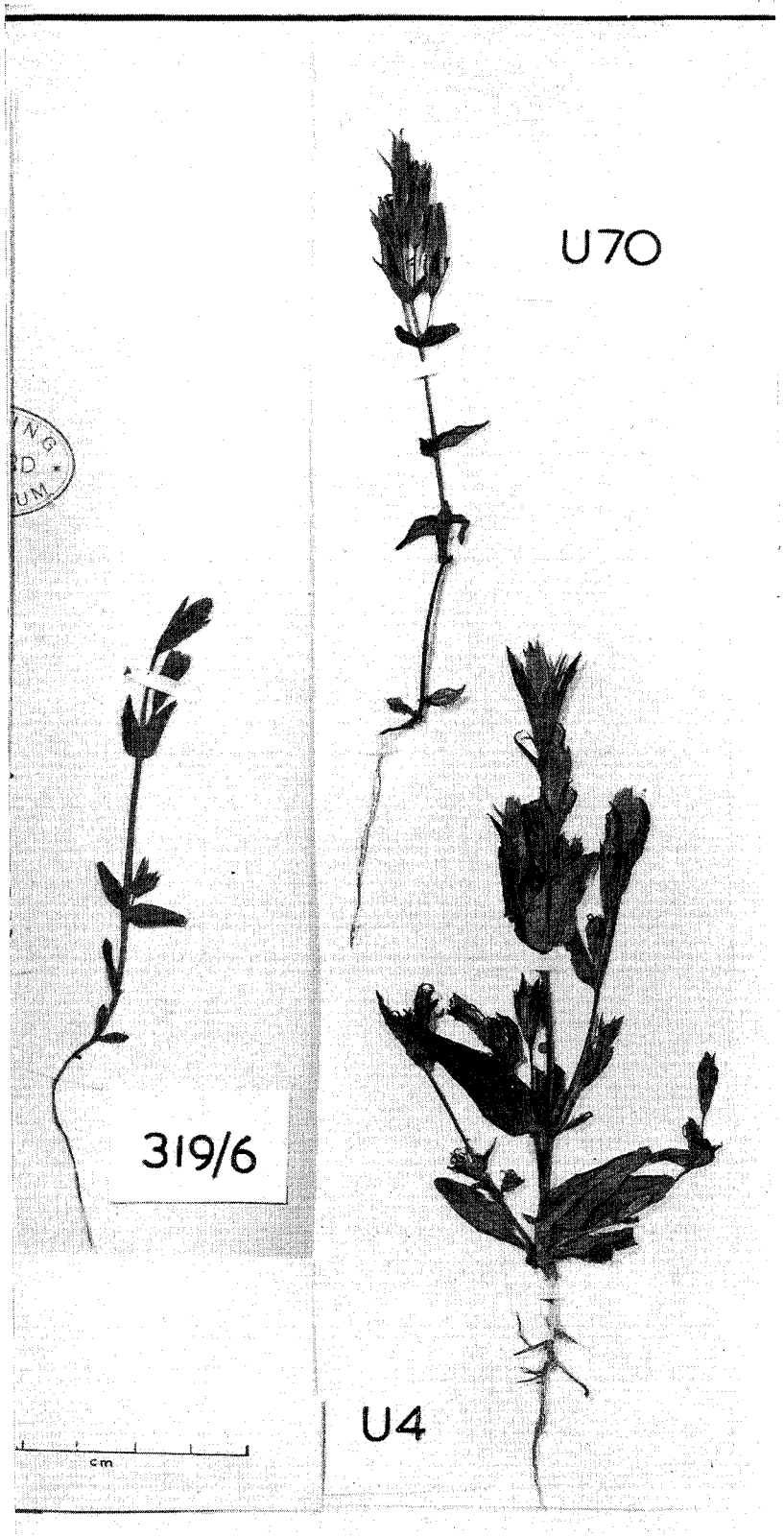


Fig. 4. *G. amarella, G. uliginosa* and hybrids : relation between terminal pedicel and height of plant.

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_1s but also probably F_2s 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 spathulate (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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