GENTIANELLA IN BRITAIN

II. *GENTIANELLA SEPTENTRIONALIS* (DRUCE) E. F. WARB.

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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 *calycina* 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) $\text{Leaf}\frac{\text{Length}}{\text{Width}}$

(4) $\text{Leaf}\frac{\text{B} - \text{A}}{2 \times \text{length}} \times 100$ (Leaf-taper Index).

(5) Inequality of the calyx, expressed in the form

$$\text{Calyx}\frac{\text{longest}}{\text{shortest}}\text{ arms} \quad \text{(Calyx-tooth Ratio).}$$

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.

	National grid reference
Random samples :	
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 $p < 0{\cdot}001$ level from its nearest neighbour.

TABLE 2
Results of "t" tests in four random samples.

		445	446	448
444 and :	*No. of Internodes*	$p < 0{\cdot}001$		
	Internode Ratio	$p < 0{\cdot}02$	$p > 0{\cdot}05$	
	Lf. L/W	$p < 0{\cdot}001$		
	Calyx-tooth Ratio		$p < 0{\cdot}001$	$p < 0{\cdot}001$
445 and :	*No. of Internodes*		$p < 0{\cdot}01$	
	Internode Ratio		$p > 0{\cdot}5$	$p < 0{\cdot}001$
	Lf. L/W			$p < 0{\cdot}001$
	Leaf-taper Index		$p > 0{\cdot}8$	
	Calyx-tooth Ratio		$p < 0{\cdot}02$	
446 and :	*No. of Internodes*			$p < 0{\cdot}001$
	Leaf-taper Index			$p < 0{\cdot}001$

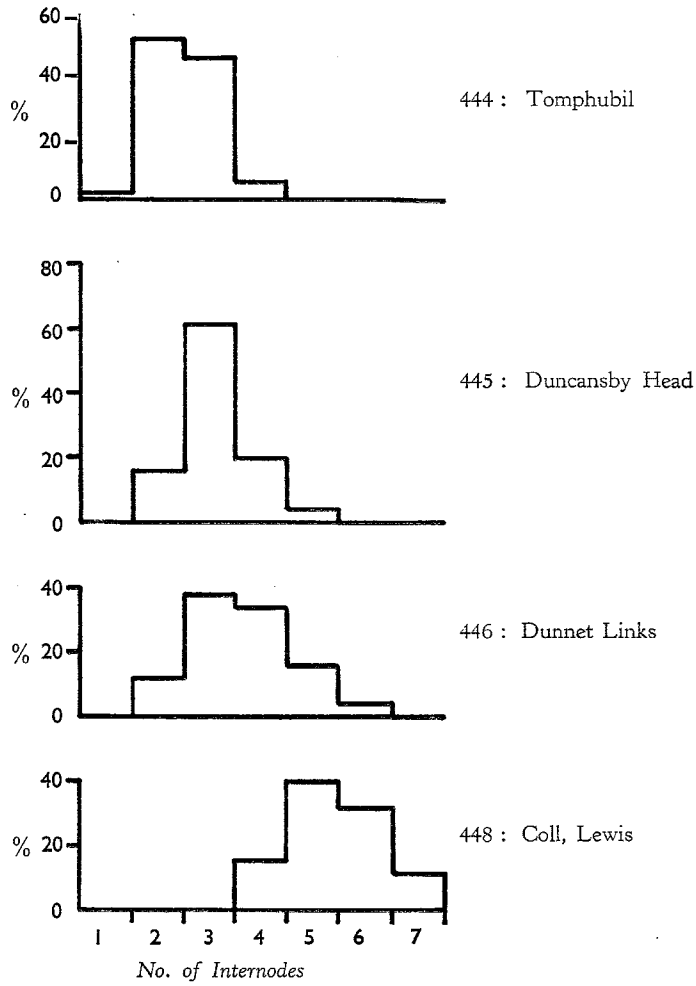


Fig. 1. Four random samples : Number of Internodes.

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.

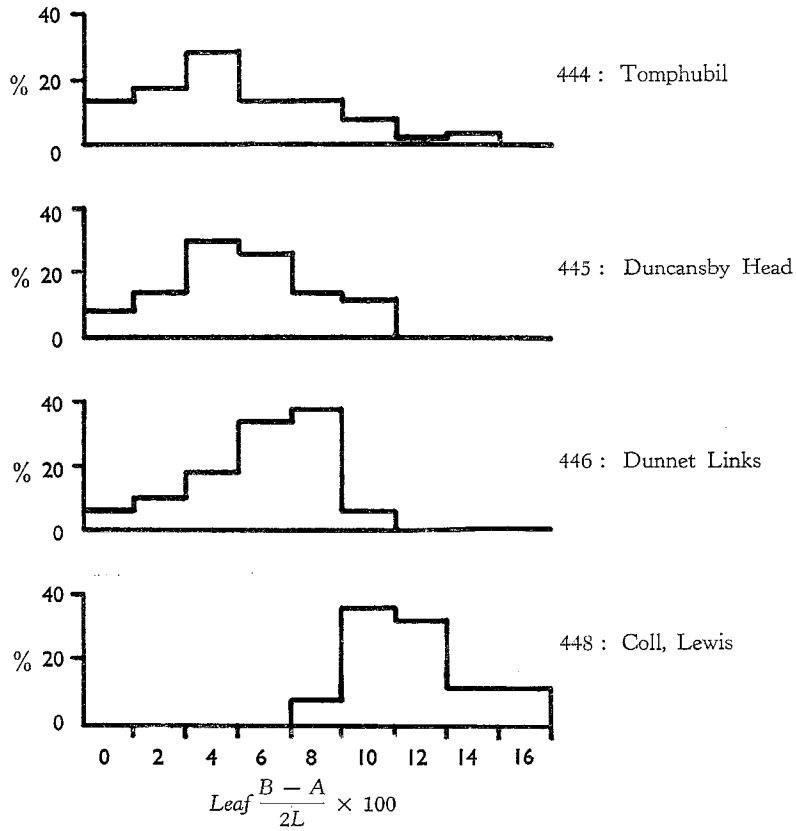


Fig. 2. Four random samples : Leaf-taper Index.

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 markep 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.

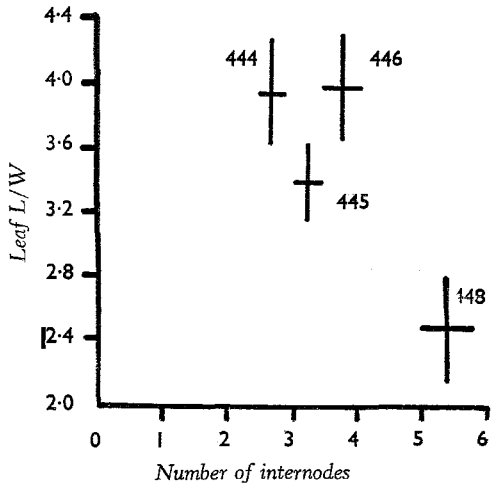


Fig. 3. Correlation of Number of Internodes with Leaf L/W.

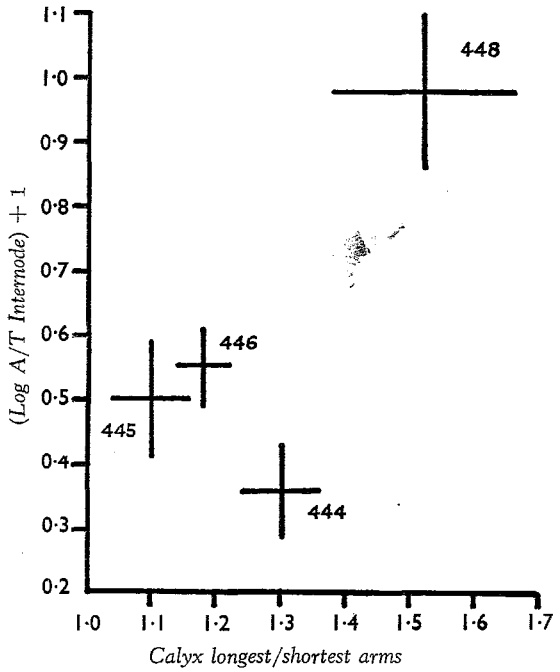


Fig. 4. Correlation of Calyx-tooth Ratio with Internode Ratio.

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).

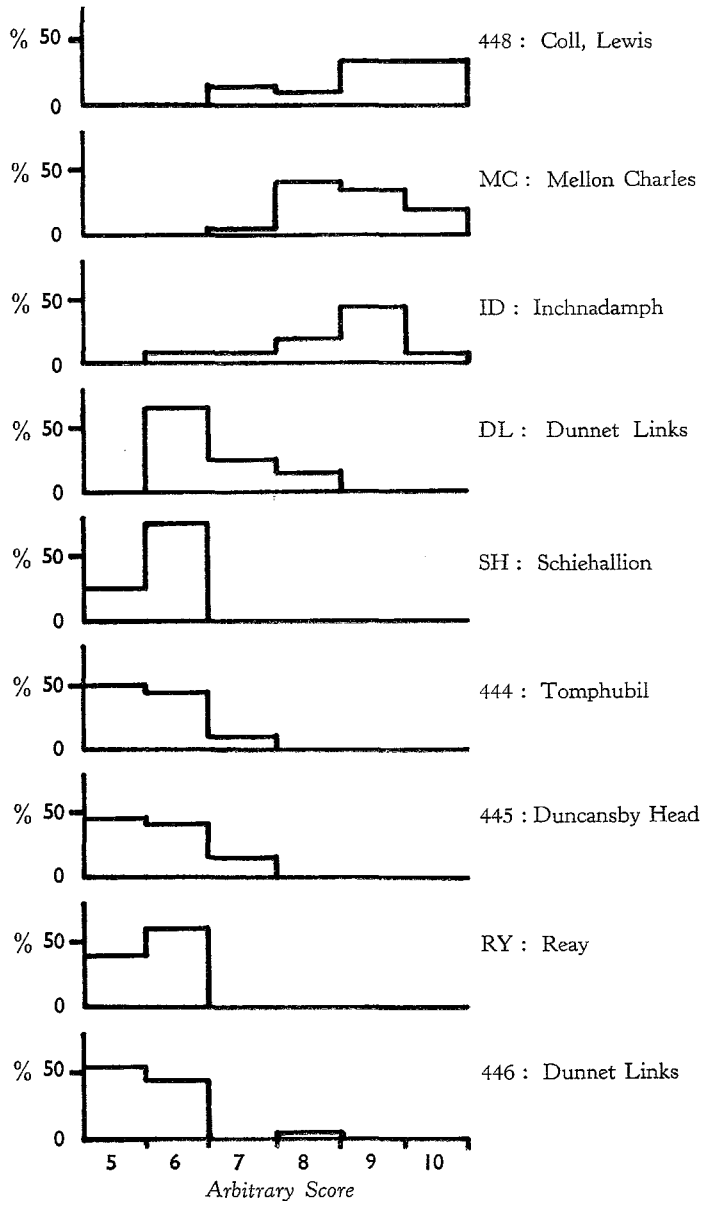


Fig. 5. Four random and five non-random samples : Distribution of arbitrary scores.

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.

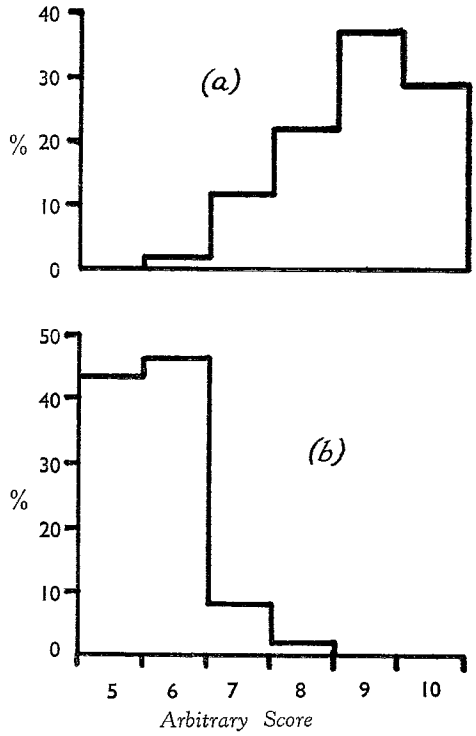


Fig. 6. Combinations of data from Fig. 5 :
(a) Western (448, ID and MC),
(b) Eastern (444, 445, 446, DL, RY and SH).

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 :

Group E; F = 24,867
Group W; F = 42,044

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.

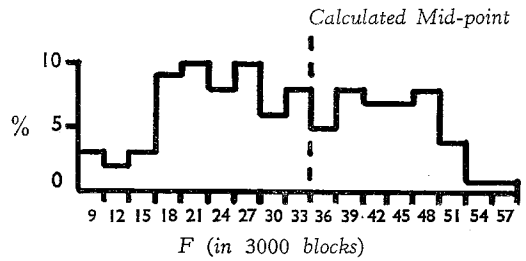


Fig. 7. Distribution of F for all specimens.

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

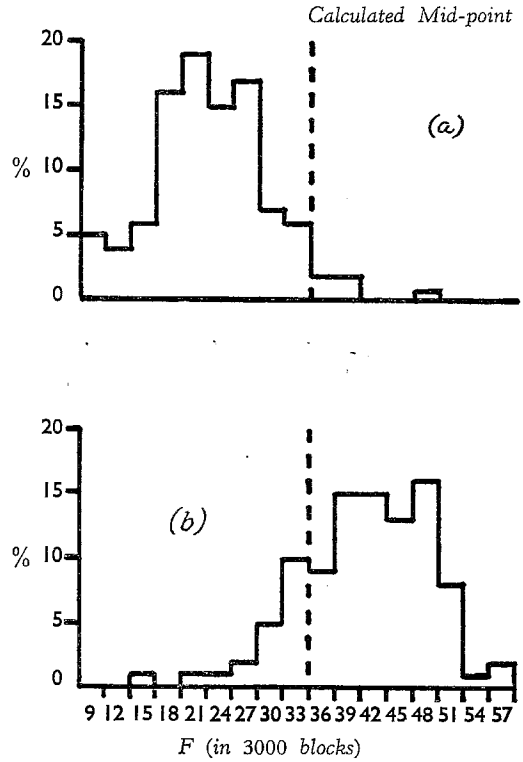


Fig. 8. Distributions of F for (a) Eastern and (b) Western groups.

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
$\text{Mean}_E + 3 \times \text{standard deviation}_E = 42{,}317$

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
$\text{Mean}_W - 3 \times \text{standard deviation}_W = 22{,}604$

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

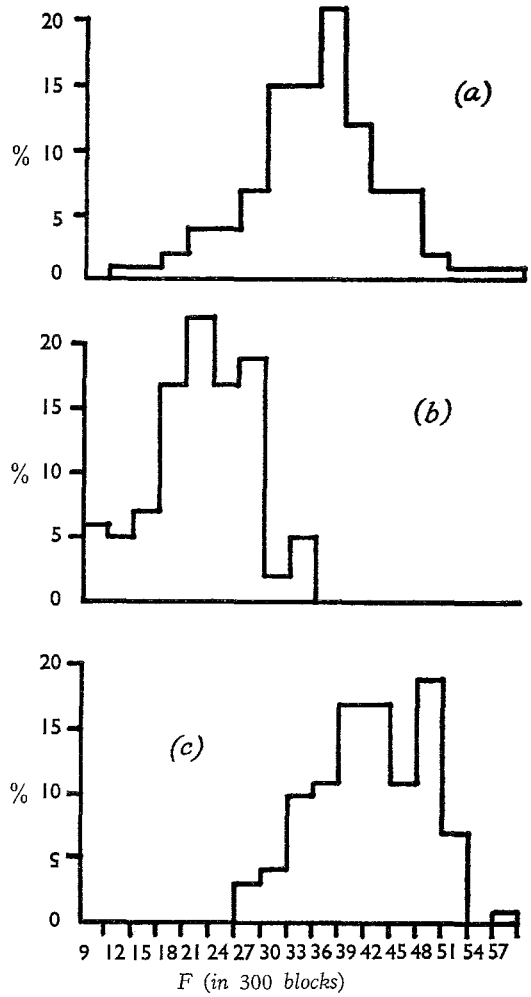


Fig. 9. Distributions of F for :
(a) All Shetland plants,
(b) Eastern group excluding Shetland plants, and
(c) Western group excluding Shetland plants.

(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.

Eastings	*Total F*	*N*	*Mean F*
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.

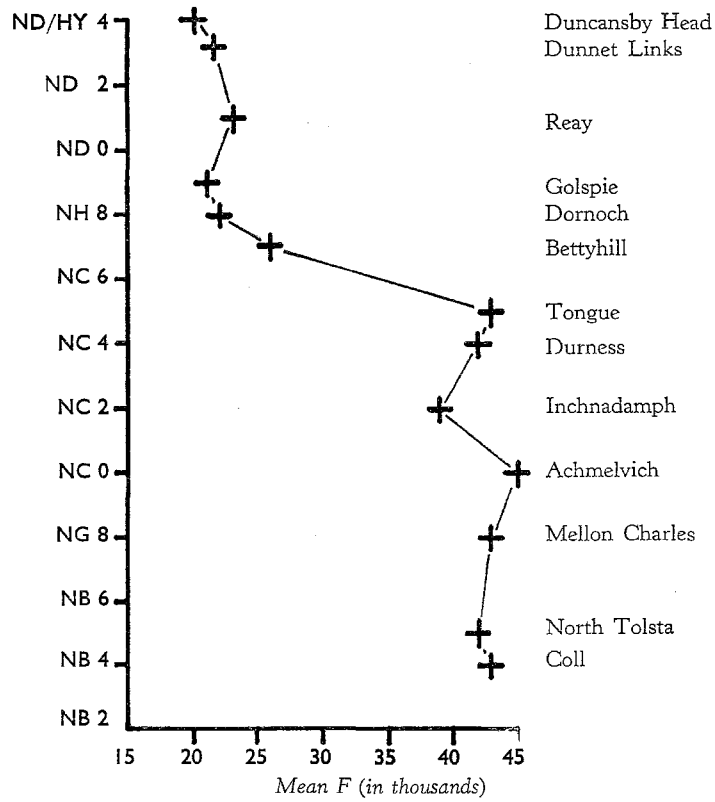


Fig. 10. Mainland and Lewis plants : correlation of F with Eastings of Grid Reference.

THE PERTHSHIRE *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.

(a) Although in 444 the plants are larger, the number of internodes is rather less (2·50 to 3·08 in 445).

(b) 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

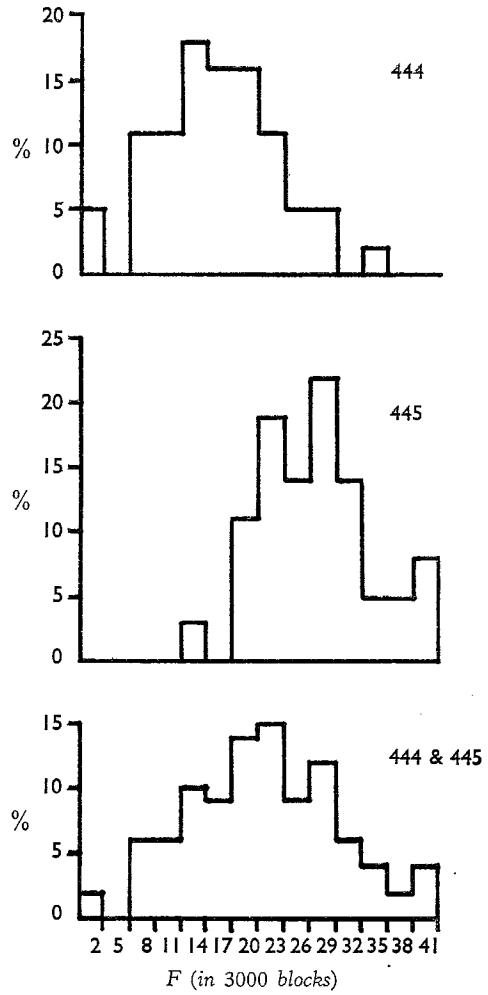


Fig. 11. Distribution of F for samples 444, 445, and 444 and 445 combined.

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 tincta; 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.

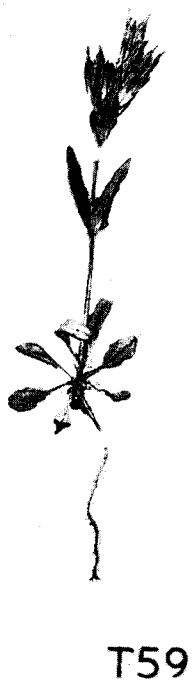
In the first citation of *G. septentrionalis* as a species (Druce, 1926) the localities given are Bettyhill and Melvich.

PLATE 15.

E24 : subsp. *druceana* (coastal race); Dunnet Links, Caithness (Holotype).

PLATE 16.

L42 : subsp. *septentrionalis*;
Spiggie, Shetland (Lectotype).



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(9?) 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 ± 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, lacinias calycis aequans vel paullum superans. Laciniae calycis valde inaequales in plantis plurimis. Corolla intus flavo-alba, extrinsecus colore purpureo-rubro saturo suffusa. Laciniae 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 subspp. *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 1½ 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 laciniae calycis circa 1½-plo longior. Calycis laciniae aequales vel subaequales, rarius inaequales. Corolla intus flavo-alba, extrinsecus colore purpureo-rubro saturo suffusa. Laciniae 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 :

(I) 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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