

GENTIANELLA IN BRITAIN

III. GENTIANELLA GERMANICA (WILLD.) BÖRNER

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SUMMARY

Gentianella germanica is taxonomically distinct from British members of the *G. amarella* aggregate, but hybridises freely with *G. amarella* subsp. *amarella*. The investigation of hybrid populations by biometric methods reveals the existence of extensive introgression. Extension of the methods to the examination of apparently pure colonies of both parent species suggests that the range of *G. germanica* was formerly more extensive than it is now, and that it is still dwindling.

ECOLOGY AND DISTRIBUTION

While *G. germanica* occurs in the same general localities as *G. amarella* there is a distinct ecological difference between the two species. *G. germanica* almost always occurs in more sheltered habitats, where the ground is less homogeneously covered with short downland turf. The most frequent situations are in slightly scrubby ground or at woodland margins; and regular associated species are *Agrimonia eupatorium*, *Chamaenerion angustifolium*, *Clinipodium vulgare*, *Crataegus monogyna*, *Festuca* spp., *Fragaria vesca*, *Helictotrichon* spp., *Hypericum hirsutum*, *Rubus fruticosus* agg., *Thelycrania sanguinea* and *Viburnum lantana*.

Colonies of *G. germanica* and *G. amarella* are often found within a few yards of each other. The differences of habitat do not seem to be absolute, and both plants may stray from time to time. Hybrids may occur throughout the range of habitats. They are often found where the ground has been altered by human activities. In the Chilterns, extensive hybrid populations sometimes occur where fields on chalk have been ploughed, sometimes up to woodland margins, or where lanes have been cut through the chalk, and the spoil thrown up in dykes. It is probable that such changes as these are partly responsible for the apparent diminution in the numbers and range of *G. germanica*.

BIOMETRIC WORK

There are many differences between *G. germanica* and *G. amarella*, and the separation of the two species normally presents no difficulty. The chief differences have been summarised by Willdenow (1797) and Wettstein (1896). In Willdenow's original description attention was drawn to the following points.

- (1) Leaves ovate-lanceolate (lanceolate in *G. amarella*).
- (2) Branches longer than the internodes.
- (3) Teeth of the (corolla) fringe ovate, acute.
- (4) Habit different.
- (5) Corolla wider and larger.

- (6) Distinctly less yellow root.

Wettstein, in his monograph of the genus, added to or amplified the description thus :

- (7) 5–15 internodes in well-developed plants.
 (8) 2nd or 3rd internode not obviously longer than the rest.
 (9) Branches in the upper (rarely lower) part, but stem usually simple.
 (10) Calyx teeth as long as or slightly longer than the calyx tube.
 (11) Calyx teeth obviously shorter than the corolla tube.
 (12) Sepals not appressed to the corolla, spreading.
 (13) Corolla 15 (in reduced specimens) – 35 mm long.
 (14) Capsule stipitatæ.

Of these characters, numbers 2, 4 and 9 relate to the habit of the plants. In *G. germanica* the branches are normally restricted to the upper nodes, and frequently form a sub-corymbose inflorescence. The pyramidal habit usually found in well-grown plants of *G. amarella* is very rare. The internodes are more or less equal, and in general shorter than at least the lower branches.

In some of the other characters the differences between the two species are not clear. No obvious distinction exists in the shape of the teeth of the corolla fringe, the colour of the roots or the length of the capsule stalks. In both species the stalks of the capsules may be up to 2 mm long. The sepals of fresh *G. germanica* are more spreading than those of *G. amarella*, but the difference tends to disappear in dried material.

The remaining differences can be treated quantitatively. The data obtained when this is done for random samples of the following eight populations of the two species and their hybrids are summarised in Table 1.

		<i>Grid Reference</i>
502 :	<i>G. amarella</i> , Beacon Hill, Oxon.	SU 7599
513 :	<i>G. amarella</i> , E. Woodhay, N. Hants.	SU 4060
514 :	<i>G. amarella</i> , E. Woodhay, N. Hants.	SU 4060
501 :	<i>G. × pamplinii</i> , Crowell Hill, Oxon.	SU 7599
511 :	<i>G. × pamplinii</i> , Ashmansworth, N. Hants.	SU 4157
512 :	<i>G. × pamplinii</i> , Ashmansworth, N. Hants.	SU 4157
504 :	<i>G. germanica</i> , Howe Wood, Oxon.	SU 6991
506 :	<i>G. germanica</i> , Letcombe, Berks.	SU 3784

From the table the following differences between the pure species are most obvious : (for explanation of the indices, see Pritchard, 1959).

(1) *No. of internodes*. Although the range in numbers of internodes overlap (largely owing to the tendency of *G. germanica* to produce slender annual forms) the means are significantly different between 502 (*amarella*) and 504 (*germanica*), the actual difference being 150.

(2) *Leaf shape*. Both leaf indices reveal considerable differences between the species. In leaf L/W the difference between 502 and 506 is 1.21, while in leaf $(B - A)/2L \times 100$ that between 502 and 504 is 4.77.

(3) *Corolla length*. This is the most striking difference between the species. In all specimens of the two examined (not only the random samples) there is very little overlap and such as there is is owing entirely to the slender forms of *G. germanica*, in which all the floral and vegetative organs are reduced in size. The difference between the means of 502 and 506 is 1.22 cms, or 76% of the mean corolla length of *G. amarella*.

(7) *Corolla/calyx ratio*. The calyx in *G. germanica* does not increase in size in proportion to the increase in corolla size. Hence this ratio is very much greater than in *G. amarella*. The actual difference between 502 and 506 is 0.47.

Similar differences are also more or less marked in the other characters shown in the

TABLE 1
Statistical data for *G. amarella*, *G. × pamplinii* and *G. germanica*

Character	<i>G. amarella</i>						<i>G. × pamplinii</i>						<i>G. germanica</i>			
	502		513		514		501		511		512		504		506	
	x	σ	x	σ	x	σ	x	σ	x	σ	x	σ	x	σ	x	σ
1. No. of internodes	6.41	1.11	5.89	0.95	6.73	1.28	8.07	1.06	6.91	1.53	7.24	1.18	7.63	1.22	8.90	1.51
2. (Log A/T Int.) + 1	1.60	0.40	1.15	0.39	1.61	0.27	1.58	0.52	1.22	0.37	1.36	0.51	1.73	0.49	1.66	0.44
3. Log Ht./T. ped.	0.89	0.24	0.66	0.33	0.94	0.23	1.03	0.15	0.73	0.25	0.67	0.26	0.82	0.31	0.84	0.20
4. Leaf L/W	3.11	1.28	3.53	0.77	2.93	0.52	3.43	1.03	2.84	0.87	2.34	0.56	2.13	0.38	2.35	0.65
5. Leaf $\frac{B-A}{2L} \times 100$	7.95	3.44	5.27	2.77	7.93	3.21	2.39	5.47	4.44	3.49	8.12	3.67	11.38	2.91	9.61	4.35
6. Corolla length	1.64	0.19	1.63	0.11	1.59	0.13	1.86	0.15	2.41	0.32	2.39	0.46	2.93	0.37	2.83	0.39
7. Corolla/calyx	1.71	0.23	1.93	0.34	1.75	0.22	1.77	0.25	2.18	0.33	1.07	0.38	2.21	0.23	2.16	0.22
8. Calyx long/short	1.10	0.13	1.09	0.14	1.15	0.17	1.29	0.33	1.10	0.10	1.06	0.09	1.09	0.10	1.10	0.11

table, except for the inequality of the calyx. (In general, when all specimens of *G. amarella* and *G. germanica* are considered, the calyx of the latter tends to be markedly less unequal). In each character, the values for the three hybrid populations are intermediate between those of the parents.

TABLE 2
t tests, *G. amarella* and *G. germanica*

Character	Samples	<i>t</i>	<i>p</i>
1. No. of internodes	502, 504	4.18	< 0.001
4. Leaf L/W	502, 506	3.81	< 0.001
5. Leaf $\frac{B-A}{2L} \times 100$	502, 504	4.18	< 0.001
6. Corolla length	502, 506	14.84	< 0.001
7. Corolla/calyx	502, 506	21.20	< 0.001

The results of *t* tests for the four characters above are shown in Table 2. The differences between the two species are highly significant in the samples and characters examined.

An examination of fairly large numbers of herbarium specimens indicated similar differences between the pure species. While the actual ranges of variation were rather greater, the two species remained distinct. Herbarium gatherings of *G. × pamplinii* are usually more or less intermediate in character, although they may range widely between the extremes set by the parent species. In the examination of *G. germanica* and *G. × pamplinii* it soon became apparent that the labelling of specimens did not always agree with their appearance. That is, many specimens of *G. × pamplinii* (recognized by eye) were labelled as *G. germanica*, and to a lesser extent, *vice versa*. Wettstein (1896) points out that backcrosses occur, and this is the impression gained from an investigation of herbarium material. The populations 513, 514, 501, 511 and 512 in Table 1 (all of which are represented by random samples) show a gradual change in general appearance, 513 being most like *G. amarella*. but with some characters of *G. germanica*, while 512 is very like, *G. germanica* but shows traces of *G. amarella* parentage. Wettstein examined the pollen of putative *G. × pamplinii*, and found a high percentage of bad grains (47%). I carried out a further examination for plants from populations 502 (*G. amarella*), 501 and 511 (*G. × pamplinii*) and 506 (*G. germanica*). The results of these investigations (for which details have already been given (Pritchard, 1959) for *G. uliginosa* etc.) are set out in Table 3. These pollen samples are again by no means random but they show a high percentage of good pollen in the parent species, and a much lower and more variable percentage in the hybrids.

Although the hybrids can usually be recognised as such, and some sort of a separation into *F*₁ hybrids and backcrosses made by eye, it seemed desirable to have some method of describing the hybrids more precisely, and thus estimating the extent to which introgression had occurred in various colonies. The results shown in tables 1 and 3 suggest introgression, and this is confirmed by field observations. First, the hybrid populations are by no means uniform, as might be expected if no backcrossing to the parents occurred. Clapham and Timm (1940) have described a situation in which no backcrossing occurs: that between *Juncus articulatus* and *Juncus acutiflorus* in the Oxford area. Here the sterile

TABLE 3
Pollen of *G. × pamplinii*

Population	% good pollen	
	Mean	σ
502 : <i>G. amarella</i> , Beacon Hill, Oxon.	96.0	1.4
501 : <i>G. × pamplinii</i> , Crowell Hill, Oxon.	61.7	5.8
511 : <i>G. × pamplinii</i> , Ashmansworth, N. Hants	53.8	8.5
506 : <i>G. germanica</i> , Letcombe, Berks.	96.0	1.4

hybrid is uniform in its morphological and cytological features. Second, a situation somewhat analogous to that in *Gentianella* is illustrated by *Nuphar × spenmerana* and *Saxifraga hirsuta × spathularis*, both of which may occur in situations where one parent is unknown. A rather similar case has been described by Yeo (1956) in *Euphrasia*, where, for example *E. vigursii* (derived from *E. anglica* and *E. micrantha*) occurs in the absence of both parents; though here there is a change in chromosome number, since *E. anglica* is diploid and *E. micrantha* tetraploid. This situation occurs frequently with *G. × pamplinii* (at Crowell Hill, Ashmansworth, etc.), where there appears to be no pure *G. germanica* remaining, although old herbarium specimens indicate that it was abundant in both localities 20–30 years ago. Third, it has been shown in Table 1 that the different populations of hybrids are not alike, varying as they do in the relative prominence of *G. amarella* and *G. germanica* characters.

Various methods of representing introgression were tried. Coded values for characters were summed, as this appeared to have been used with some success by Morton (1956), for hybrid colonies of *Ononis repens* and *O. spinosa*. Pictorial methods were attempted, of the types used by Anderson (1949) in separating introgressed colonies of north American irises. None of these gave a useful separation, although Anderson's methods were rejected mainly because of the dependence of the method on random samples, and the fact that the ranges of variation of the parent species in most cases showed considerable overlap.

A method was required which would give a composite figure for small samples of hybrids, and since for the greatest value this figure should be a linear function, experiments were made with discriminant analysis. This has already been described in some detail, as the method used to separate two taxa within *G. septentrionalis* (Pritchard, 1960). Here the aim is somewhat different: there is no difficulty in separating the parent species, but a function is required to assess the apparent parentage of hybrid plants.

Of the characters available for the analysis, three were eventually selected. These were:

- s*, number of internodes
- e*, leaf L/W
- o*, corolla/calyx ratio.

A trial discriminant analysis was carried out in which a fourth character, *k*, corolla size, was used in place of the corolla/calyx ratio. It was apparent that hybrids could be detected by several features, for example intermediacy in characters *s*, *e*, *k* and *o* above, and that these were not necessarily closely correlated. When corolla size was used in the analysis, it was found that its discriminant value was so high that its effect completely swamped those of the other characters. Thus, a population whose corolla size closely resembled that of *G. amarella* would have a discriminant function approximately equal to that of *G. amarella*, although it might be intermediate in, say, leaf shape. Conversely, a population

resembling *G. amarella* in all respects except corolla size would nevertheless be discriminated as *G. germanica*. Scarcely any separation is gained from the discriminant function beyond that obvious from corolla length alone.

This points out a difficulty and limitation in the use of discriminant analysis. Although the method weights each character according to its numerical values, this weighting is not necessarily related to its taxonomic value. If the numerical differences are too great in one character, then the discriminant analysis will virtually ignore those whose differences are less, but perhaps of equally great taxonomic value. It is necessary to select characters whose apparent numerical values are approximately equal. In this case, although the difference in corolla size between *G. amarella* and *G. germanica* is large and constant, its discriminant value when applied to hybrids is taxonomically little if any greater than that of other characters.

The use of discriminant analysis to analyse hybrid populations, although basically similar to its use for separating distinct, non-hybridising, taxa has certain important differences. Figures 1–3 show the distributions of characters for (a) southern *G. amarella* (populations 502 and 515 combined); (b) hybrids (populations 501, 511 and 512); (c) *G. germanica* (populations 504 and 506), and (d) a combination of (a), (b) and (c). The characters shown are (s) no. of internodes, (o) corolla/calyx ratio and (e) leaf L/W.

From these histograms it can be seen that the frequency distributions of characters for *G. amarella* and *G. germanica* are distinct, whereas those for the hybrids are intermediate.

When the frequency distributions are combined (Figs. 1 (d), 2 (d), 3 (d)) curves

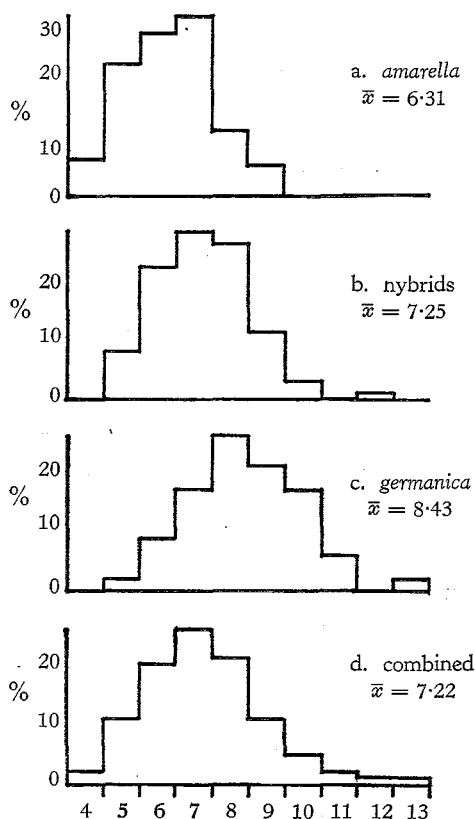


Fig. 1. Number of internodes in *G. amarella*, *G. germanica*, and hybrids.

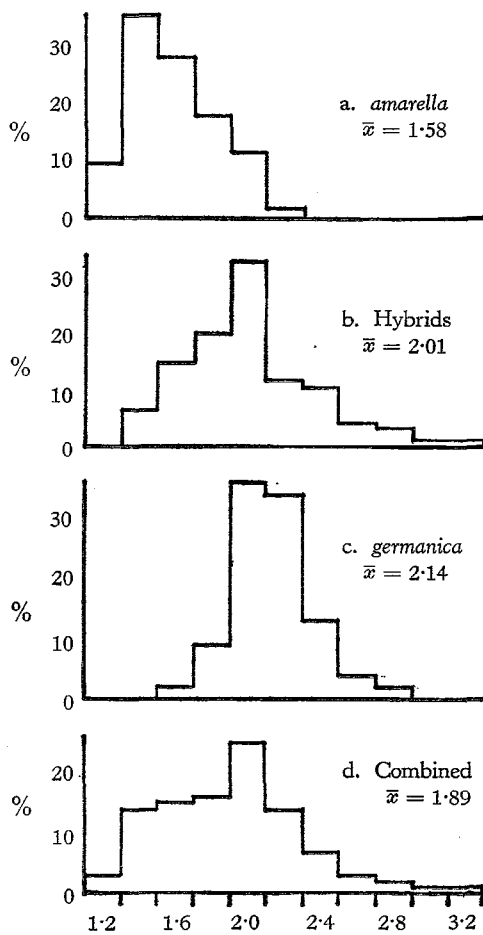


Fig. 2. Corolla/calyx ratio.

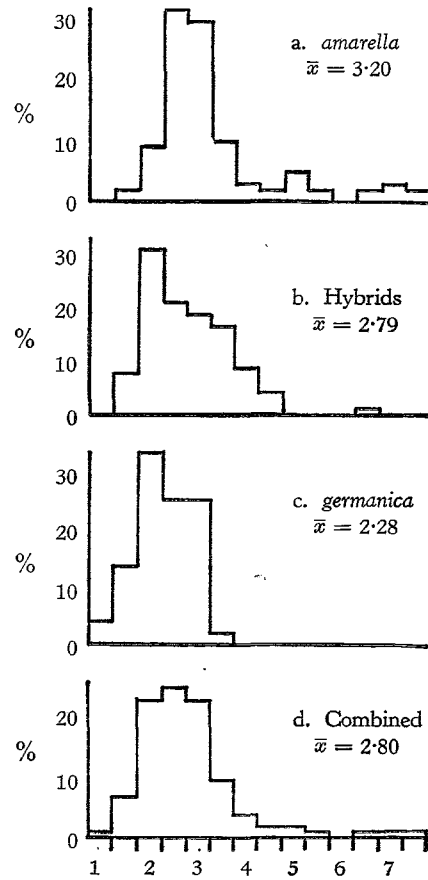


Fig. 3. Leaf length/width.

are obtained which are approximately unimodal. This indicates that, taken together, the two parent species and their hybrids form a large population with its variation about a single mode. The same conclusion is suggested when all herbarium specimens are treated similarly.

The calculation of the discriminant function requires the establishment *a priori* of a number of primary groups. In the first place, these primary groups were taken as the parent species, and no account was taken of the hybrids in the calculation. The discriminant functions of the hybrids could then be derived from the coded values of characters for each plant and the weighting factors obtained from the parent species. This method gave a reasonably satisfactory distribution of the discriminant functions for the hybrids. It was however, subsequently suggested (Finney, personal communication) that a better separation might be obtained by using recognisable groups of the hybrids as some of the primary groups, and this proved to be the case. The calculation of the weighting factors is the same as in the case of *G. septentrionalis* (Pritchard, 1960). The weighting factors eventually obtained are shown in Table 4.

TABLE 4. Weighting factors

No. of internodes	+ 2.4859	$\approx + 2.5$
Corolla/calyx ratio	+ 3.0296	$\approx + 3.0$
Leaf L/W	- 1.0000	$= - 1.0$

The mean values of the discriminant function for each of the random samples, together with certain combinations of these, are shown in Table 5. The order of the samples within the table is that of their apparent parentage judged by eye. With the exceptions of the two pairs of samples from East Woodhay and Ashmansworth this is also the order of their discriminant functions.

(1) The mean value for 502 and 515 is 116.5, rather less than that for A1–A106 (129.9). These are colonies of apparently pure *G. amarella*, and this value may be taken as that for southern *G. amarella* as a whole.

(2) When the total includes 513 and 514, the mean rises to 129.9, the combined mean of these two samples being 150.4. During work on *G. amarella* (Pritchard, 1959) it was felt that certain chalk populations, these two included, showed divergences from the majority. These divergences are all of the sort evident in 513 and 514. They indicate a degree of introgression from *G. germanica*, which is abundant in the area, although not now found in the immediate vicinity of populations 513 and 514.

TABLE 5
Mean values of F for random samples of *G. amarella*, *G. germanica* and hybrids

Nos.	Population	Mean value of F
A1–31	502 : Beacon Hill (23)	116.3
A74–106	515 : Abinger (17)	116.7
A32–56	513 : E. Woodhay (12)	154.0
A57–73	514 : E. Woodhay (12)	145.0
P58–72	501 : Crowell (23)	176.3
P26–57	511 : Ashmansworth (12)	223.7
P1–25	512 : Ashmansworth (12)	222.9
G1–16	504 : Howe Wood (23)	256.9
G17–47	506 : Letcombe (22)	276.0

(3) 501 resembles *G. amarella* in a general way although several characters suggest introgression from *G. germanica*. The latter species was formerly plentiful in the same locality. This is in good agreement with the sample's discriminant function of 176.3 which is closer to *G. amarella* than to *G. germanica*, being below the calculated mid-point of 196.4.

(4) The field inspection suggested that 511 and 512 contained a large proportion of F_1 hybrids. The theoretical F for F_1 hybrids should be 196.4, the calculated mid-point, but the value for 511 and 512 of 223.3 is rather above this.

(5) Between 504 and 506 certain differences have been noted, such as the lower number of internodes in 504. The values of F (256.9 and 276.0) again suggest introgression from *G. amarella* in 504, which agrees with field observations. Owing to the presence of *G. amarella* only about 50 yards from the Letcombe colony, it may well be that the value for pure *G. germanica* would be even higher than 276.0.

Thus the discriminant function provides a reliable guide to the parentage of random samples of hybrid populations, confirming field observations and impressions. Figure 4 shows the distribution of F for the random samples. 502 and 515 are treated as *G. amarella*, 513 and 514 as "amarelloid" hybrids, 501, 511 and 512 as hybrid colonies containing

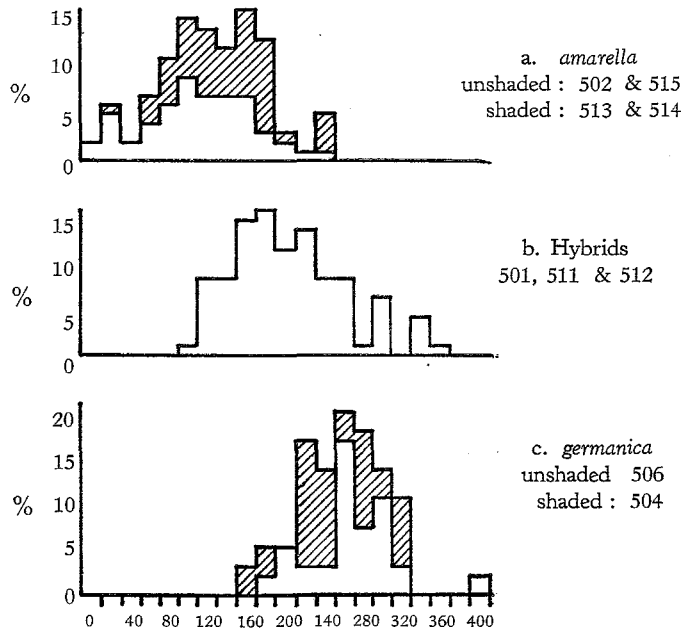


Fig. 4. Distribution of F for random samples of *G. amarella*, hybrids, and *G. germanica*.

more or less of each parent and 504 and 506 as *G. germanica*, 504 showing slight introgression from *G. amarella*. From the histogram it is clear that a good separation is obtained. The actual overlap between pure *G. amarella* and pure *G. germanica* is only 19%. If 513, 514 and 504 are included, the overlap rises to 40%. The hybrids occupy an almost exactly intermediate position.

In 504 and 506 the mean F falls just outside the overlap. In 502, 513, 514 and 515 it is well outside. (The values for 506 alone and for 502 and 515 are of course further away). Coupled with the shape of the histograms, these figures suggest that in the plants so far considered, "pure" *G. amarella* (i.e. 502 and 515) is "purer" than "pure" *G. germanica* (i.e. 506). This is borne out by examinations of herbarium material; traces of introgression can often be seen in *G. germanica*, but rarely in *G. amarella*. This is partly owing to the tendency of botanists to separate hybrids (as *G. × pamplinii*) from *G. amarella* more readily than from *G. germanica*. For example, a larger corolla and ovate-lanceolate leaves are more striking in a population of *G. amarella* than are a smaller corolla and lanceolate leaves in one of *G. germanica*. Further, the geographical range of *G. germanica* in Britain lies entirely within that of *G. amarella*, which is very much wider.

An analysis of herbarium material reveals several interesting points. In Table 6 plants from southern chalk and limestone localities are split into four groups :

- (a) Plants from known *G. germanica* areas.
- (b) Plants from chalk areas where *G. germanica* does not grow (excluding (c) below).
- (c) Plants from Surrey, Kent and East Sussex.
- (d) Plants from oolite localities.

Group (d) has the lowest value, which is similar to that for the random samples of *G. amarella* (117). Group (b) comes next, and its mean value is not significantly different ($p > 0.05$) from that of pure *G. amarella*. Group (a) has the highest value, slightly higher than that of the Crowell hybrids (501 : mean F = 176). There is a tendency for

TABLE 6

Group	Range of F	Mean F
(a)	75-251	179
(b)	21-226	135
(c)	56-256	157
(d)	69-169	115

collectors to gather large and striking plants for their herbaria, and these are just those which are most likely to show introgression from *G. germanica*. It must be concluded that introgression is widespread in the areas in which the two species occur together.

Group (c) was separated from Group (b) because the plants showed some of the characters of *G. germanica* in small measure. The mean F for these plants is considerably higher than that of group (b) and approaches that of group (a). There are two possible inferences from these data. There may be local variation in *G. amarella* in S.E. England, which does not seem unlikely. However, no such variation appears to occur elsewhere within the range of the chalk and southern limestone race of *G. amarella*. Alternatively, the data may indicate earlier introgression from *G. germanica*. Although apparently suitable habitats abound in Surrey, Kent and Sussex for this species, similar to those in which it is found in the Chilterns, it does not now occur in Britain east of Hertfordshire, Buckinghamshire and Berkshire. Many plants placed by Matthews (1955) in the Continental element of the British flora (e.g. *Cirsium acaule*, *Ophrys insectifera*) occur with *G. germanica* in its present habitats and also extend along the North and South Downs. In view of the European distribution of *G. germanica* (mountains of central, north and east central Europe) it is surprising that it does not occur in S.E. England. Further, it has been shown that in some localities where undoubted hybrids are found, and whence *G. germanica* has in the past been recorded, it no longer occurs. It seems probable that this species did once occur on the Downs, and that over a long period introgression with *G. amarella* has obliterated all but traces of it. (Cf. *G. uliginosa* in South Wales (Pritchard, 1959)).

Tables 7 and 8 show the means of F for a number of small herbarium samples of *G. germanica* and *G. × pamplinii*, grouped according to the herbarium labelling. The column headed "appearance" is my own estimation of the sample's parentage.

Of the samples labelled *G. germanica*, all except four (657-61, 72-4, 102-4 and 105) appear more or less pure, while three (G 85-9, 119 and 137-8) are nibbled and show low values of F. The mean value for all these samples, excluding those seven but including P 81-82 (labelled *G. × pamplinii*) is 279, very slightly higher than that of sample 506 (276). *G. amarella* is not a common plant in those parts of Buckinghamshire (the Chiltern scarp) where *G. germanica* is abundant, primarily owing to the scarcity of open grassland free of scrub. It is therefore of some interest that the mean value for Buckinghamshire plants is 314, rather higher than that for the plants as a whole. After removal of the Buckinghamshire plants the mean of the rest is 262. For those localities in which I know that *G. amarella* also occurs, the mean value is 256 (plants from Crowell, Letcombe, Ashmansworth, Waterslip, Chinnor, Shelbourne and Assenton).

Among plants of *G. × pamplinii* (G 57-61, 72-4, 105, P 73-80, 83-117) the mean value is 207. Only six samples differ from the mean by more than 20 points. Of these, P 92-4 and 114-5 are apparent backcrosses (*G. germanica* × *G. × pamplinii*) while P 85-6 and 116 are slender annual forms. If these are omitted, the mean value for *G. × pamplinii* is 204.

TABLE 7
Specimens labelled *G. germanica*

Nos.	Date	Appearance	Mean F
G 48-50	1820	G	288
51- 4	1879	G	339
55- 6	1898	G	307
57-61	1897	AG	211
62-71	1883	G	255
72- 4	1892	AG	220
75- 6	1903	G	273
77	1915	G	298
78-80	1923	G	289
81- 2	1923	G	325
83- 4	1895	G	204
85- 9	1927	G (nibbled)	248
90- 2	1890	G	266
93-101	1892	G	229
102- 4	1883	aG	264
105	1917	AG	227
106- 8	1878	G	300
109-11	1904	G	384
112- 8	1913	G	296
119	1921	G (nibbled)	157
120- 5	1910	G	227
126	1913	G	295
127	1913	G	297
128-30	1930	G	241
131- 5	1931	G	339
136	1941	G	272
137- 8	1941	G (nibbled)	147
139-41	1941	G	309
142- 4	1942	G	302
145-52	1894	G	246
153- 5	1937	G	306
156- 7	1864	G	303

Appearance : G = *G. germanica*
aG = hybrids resembling *G. germanica*
AG = more or less intermediate

While these samples are neither random nor, probably, uninfluenced by collectors' bias, after the above corrections the following relationship emerges :

- (a) Mean F for 'corrected' *G. amarella* (random samples 502 and 515) = 117
(b) Mean F for 'corrected' *G. × pamplinii* (as above) = 204
(c) Mean F for 'corrected' *G. germanica* (Buckinghamshire plants) = 314

The average of (a) and (c) is 216, and if (a) and (c) represent pure species, this would be the expected value for (b). The actual value is not much lower than this.

It seems that pure *G. amarella* colonies are easiest to find, largely owing to the much wider range of this species. Pure *G. germanica* is much more elusive, and probably the best remaining localities are those on the scrubby slopes of the Thames Valley in Bucks. Throughout the rest of the range of *G. germanica*, *G. amarella* also occurs, and is usually the commoner species. The two species hybridise freely, and the F_1 is quite fertile, with the result that hybrid swarms occur and introgression is marked. In some places (Crowell

TABLE 8
Specimens labelled *G. × pamplinii*

Nos.	Date	Appearance	F
P 73-80	1946	AG	210
81- 2	1917	G	259
83- 4	1892	AG	207
85- 6	1892	AG	155
87	1895	AG	214
88-91	1913	AG	204
92- 4	1913	aG	261
95- 8	1915	AG	187
99-109	1910	AG	186
111- 3	1921	AG	236
114- 5	1897	aG	282
116	1915	AG	115
117	1889	AG	213

Hill, East Woodhay, Kent) this has proceeded so far that *G. germanica* can no longer be found, but the remaining *G. amarella* shows distinct traces of past introgression. A new use of the method of discriminant analysis has rendered the analysis of such populations less subjective, and confirms observations made in the field.

TAXONOMY

GENTIANELLA GERMANICA (Willd.) Börner (1912); *Gentiana germanica* Willd. (1797); *Gentiana Amarella* var. α Froelich (1796); *Gentiana Wettsteinii* Murb. (1892).

Linnaeus (1753) did not distinguish between *G. amarella* and *G. germanica*, though it has earlier been remarked that there are specimens of both species in Linnaeus' Herbarium (Pritchard 1959). Froelich (1796) amplified Linnaeus' description in such a way as to suggest that it referred to *G. germanica*, though he gave six varieties. Froelich's description of the type follows in part (translated) :

“Stem . . . faintly hexagonal, purplish, with branches in the leaf axils. . . .
Cauline leaves sessile, very slightly connate, ovate or ovate-lanceolate, acute or sub-acute; the uppermost ones subcordate, acute. . . . Flowers an inch long.
. . . . Corolla . . . purplish-blue . . . five-toothed, with ovate-lanceolate teeth about . . . of the corolla-tube in length.”

In this description the distinctive characters of *G. germanica* are listed, and in his original publication of the name Willdenow (1797) includes as a synonym of *G. germanica* Froelich's *G. Amarella* excluding varieties.

Froelich did however, use the name *germanica* for his varieties β and α of *G. campestris*. For this reason Murbeck (1892) published the name *G. Wettsteinii* to replace *G. germanica* Willd., and this change was retained by Wettstein (1896). Since Froelich used the epithet only for a variety, Willdenow's name is correct.

The British specimens of *G. germanica* are indistinguishable from the Continental plants. No specimens seen by Willdenow, or his type, have been seen, but a number of the exsiccata cited by Wettstein and plants seen by him have been examined. These are : (cited) *Reliquiae Mailleanae* no. 862, *Herb. d. Fl. loc. d. Fr.* no. 68, and (labelled

"Revidit R. v. Wettstein"), Dörfler *Herb. Norm.* nos. 3755 and 3756. There is no confusion about the identity of the British plant, and no change is proposed in the status of the species.

Geographical Distribution

Wettstein gives the Continental distribution of *G. germanica* as: Sweden, England (Harefield and Letcombe Castle), north and east France, Belgium, Germany, Austria-Hungary, Switzerland.

In Britain, the plant is restricted to the chalk of south-east England. I have seen specimens from the following vice-counties: 7, 12, 20-24, 30.

Druce (1932) gives in addition the following vice-comital records for *G. germanica*: 5, 8, 17, 19, 45, 51, 57. Of these, 5 seems scarcely likely as it is completely away from the chalk, but the possibility must be borne in mind. 17 in particular is quite possible. 19 again is possible, but 45, 51 and 57 seem improbable.

No trace of the record for v.c. 57 can be found. That for vice-county 51 was made by Dallman (1908) for "The Marian, Cwm," and for "Limestone common skirting the road East of Glol, alt. 700'." No further records nor specimens have been traced from either of these localities. The Tenby record (v.c. 45) was made by Falconer (1848). Hyde (personal communication) considers the record probably mistaken, as no sign of the plant has been seen since.

GENTIANELLA × *PAMPLINII* (Druce) E. F. Warb. (1952) = *G. amarella* × *G. germanica*; *Gentiana* × *Pamplinii* Druce (1893); *G. axillaris* × *G. Wettsteinii* (Wettstein 1896).

In 1893 Druce described what he believed to be a hybrid, *G. amarella* × *germanica* = *G. × pamplinii*, from Letcombe Castle in Berkshire. He remarked that in the locality a good deal of *G. amarella* continued in flower with *G. germanica* (this is probably largely due to introgression; there is normally only a slight overlap between the two species). He stated that the obconical corolla tube of *G. germanica* fully distinguished it from the nearly cylindrical tube of *G. amarella*, and that the hybrid was certainly somewhat intermediate in character. The specimen was sent to Wettstein, who described in it 1896. Druce (1896), having by then had a reply from Wettstein, further described the hybrid thus. "(The plants) had a longer and more conspicuous corolla than *G. Amarella*. The corolla was more cylindrical than that of *G. germanica*, and the tint was nearer the dark purple of *Amarella* than the bluish purple of *germanica*. The pollen was defective, and the plant was in my opinion distinctly a hybrid of the two species with which it occurred,"

The specimen is in the Druce Herbarium at Oxford, labelled "*Gentiana Amarella* × *germanica*, Letcombe Castle, Berks., Sept. 1892. G. C. Druce and B. Taylor." It is also labelled on the sheet "Type Spec." in Druce's handwriting.

The distribution of those plants I have seen is v.c.'s 7, 12, 22-24.

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