GERANIUM PURPUREUM VILL. AND G. ROBERTIANUM L. IN THE BRITISH FLORA

I. GERANIUM PURPUREUM

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Geranium purpureum Vill. and G. robertianum L. form a valuable pair of species for ecological and cytogenetical comparison. One is a rare species whose British occurrences are at the northern limit of its Mediterranean type of distribution while the other is a widespread species with a considerable range of ecological tolerance. Since 1945 they have been grown, observed and hybridised in the Experimental Gardens of the University of Leeds. The genecological results of this study will be published elsewhere; in the present papers the subspecific units which have been established in each species as a result of the experimental and field studies are treated taxonomically and their British distributions are mapped.

A great many infra-specific taxa have been described for these two species by those who have only observed their plants in the wild. Cultivation experiments show that some of these have no genetical basis (and are modifications induced directly by the environment). Only those distinctions which are maintained in cultivation in the uniform conditions of a garden are to be considered worthy of nomenclatural recognition. With this principle in mind, those morphologically distinct forms which appear to be ecologically significant (or to possess a distinctive geographical distribution) are given subspecific rank. They are the 'ecological races' and their taxonomic treatment is thus in accordance with the principles of Clausen, Keck & Hiesey (1939). Within these subspecies, lesser morphological groupings may be made, but these more or less discrete forms usually differ from each other only in respect of individual qualitative characters. They are accompanied by other, more or less continuous, variation in quantitative characters and neither the discrete nor the continuous variation within the subspecies appears to have any measurable ecological correlation.

On this basis, British material of *Geranium purpureum* appears to consist of two subspecies, while *G. robertianum* contains three (which will be discussed in the second paper of this series). That there are other non-British infra-specific groupings in both species is certain and some of them will be treated elsewhere.

In the preparation of these accounts, use has been made of material contained in the following herbaria:—

H. G. Baker	(Bak.)	Royal Botanic Gardens, Kew	(K)
British Museum (Natural History)	(B.M.)	Borrer at R.B.G., Kew	(K.Borr.)
Boswell-Syme at B.M. (N.H.)	(B.M.Bosw.)	Cryer at Leeds University	(L.Cry.)
Sowerby at B.M. (N.H.)	(B.M.Sow.)	Roper at Leeds University	(L.Rop.)
Cambridge University	(Cam.)	Oxford University	(Ox.)
Marshall at Cambridge University	(Cam.Mar.)	National Museum of Wales, Cardiff	(WNH)
Royal Botanic Garden, Edinburgh	(E)	C. C. Townsend	(Towns.)
Royal Albert Museum, Exeter	(Ex.Hiern)	Muséum National d'Histoire Naturelle, Pa	ris (Par.)

Grateful acknowledgment is made to the authorities concerned.

Geranium purpureum Vill. (1785), Fl. Delph., 72, emend. Jord. (1848)

- G. PURPUREUM subsp. PURPUREUM
 - G. scopulicolum Jord., nom. nud.
 - G. lebelii Boreau (1840), Fl. Cent. Fr., 1, 324.
 - G. modestum Jord. (1848), Adnot. Cat. plant. Jard. Grenob., 3; (1860), Bull. Soc. Bot. Fr., 7, 605.
 - G. minutiflorum Jord., Cat. Dijon; ex ej. (1848), Pug. Pl. Nov., 39.
 - G. robertianum L. var. modestum Syme, 1863, Eng. Bot., ed. 3, 2, 204, t. 306.
 - G. intricatum Gren. in litt. et in herb. Mus. Paris; ex Rouy (1897), Fl. Fr., 4, 98.
 - G. purpureum Vill. var. genuinum Rouy (1897), Fl. France, 4, 97.

Type locality: Pont de Claix, near Grenoble, France.

Within the species Geranium purpureum as defined by Villars, there were two distinct plants, one from Le Buis (Drôme) the other from the Pont de Claix, near Grenoble. Jordan (1848) recognised this and redefined G. purpureum on the basis of the Pont de Claix form, separating the material from Le Buis as G. villarsianum. The former contains plants whose fruits carry a pattern of ridges on their backs while the latter group of forms is characterised by thick weals on the fruits. In the Paris herbarium there are several sheets from Pont de Claix. Jordan, however, came to believe that any units which were distinct, constant and true-breeding represented true species and, as a result of the cultivation experiments which he carried on with plants of various genera, he described a great number. Because G. purpureum is normally self-pollinated, it tends towards homozygosity and, while populations in any locality may be relatively uniform as a result, there are often well-marked distinctions between populations (Baker, 1953). Consequently, Jordan, after cultivating samples of some of these populations, was able to describe at least two new "species" within this group. Other French workers were willing to find specific diversity here. Wilmott (1921) has already pointed out that G. purpureum, G. scopulicolum, G. modestum and G. lebelii cannot be separated by any character which we should now consider to be of specific significance. Indeed after the examination of authentic material from French sources, both in British Herbaria and at Paris, they do not seem to differ even in subspecific degree from Villars' type. G. minutiflorum appears to represent an exposed form of this subspecies. G. intricatum, which is characterised by the extreme reduction in size of the leaves in the region of the inflorescence, also appears to represent only a minor variant. None of them have significantly different ecological preferences and they occur here and there within the general area of the species.

Thus, within the limits of the species, the type subspecies may be said to comprise plants which have an upright or strongly ascending habit and grow in rocky places, on cliffs and on dry hills. In the southern parts of its distribution these plants may occur in shady places, even in woodland, but in the British Isles they are rather intolerant of shade. Except in some populations where hybridisation with G. robertianum appears to have played a part, their fruits carry a characteristic pattern of closely-set ridges (Fig. 1). These fruits may be glabrous or hairy.

This subspecies ranges through south-western and western Europe and reaches the islands of Madeira. Its complete European distribution is not yet fully worked out but it is replaced in many Mediterranean areas by the group of forms included in *G. villar-sianum* Jord. and in the eastern Mediterranean and the highlands of East Africa by a third species which has also been confused with *G. purpureum*.

As indicated by Evans (1920) and Wilmott (1921), plants agreeing in all essentials with Villars' type are found in all the south-western stations for the species in the British Isles. Here they grow particularly in rocky and stony places (but are also found in open

hedgebanks), usually near the sea, and always in a rich soil (usually derived from a limestone). Their British and Irish distribution is thoroughly in accordance with that of the Mediterranean element in our flora.



Fig. 1. Dorsal view of fruit of G. purpureum Vill. subsp. purpureum from Leigh Woods, N. Som. (× 20).

The detailed distribution of this subspecies is as follows. Collectors' names are given only for the less well-known localities.

CHANNEL ISLES:

- JERSEY: St. Helier, 1838, Babington (Cam.); La Haule; St. Brelade's; Don Bridge, 1923, Barton (B.M.); Quenvais; St. Peter's, 1923, Barton (B.M.); St. Ouen's; St. Anne's, 1920, Druce (Ox.); Port Mogurta, 1906, Druce (Ox.); L'Etac, Lester-Garland in Fl. Jersey, 1903, is undoubtedly correct.
- GUERNSEY: Fort George, 1926, Foggitt (B.M.); S.W. Guernsey, 1879, Melvill (B.M.); E. of Vazon Bay, 1878, Fraser (Ox., WNH); around Cobo Bay, 1878, Fraser (K), 1923, Foggitt (B.M.); Grandes Rocques, 1912, Barton (B.M.); Bordeaux Harbour, 1902, Cooper (Ox.); Vale Castle, 1883, Fawcett (B.M.); 1906, Druce (Ox.); Paradis, 1897, Druce (Ox.). King's Mills, Grosse Hougue and Spur Point, Marquand, Fl. Guernsey, 1901, are probably correct.
- V.c. 1. W. CORNW.: Scilly Isles (probably St. Mary's), 1878, Curnow (WNH); Hayle, 1922, Pegler (B.M.); around Crantock and Newquay; Padstow.
 - E. CORNW.: Wadebridge; St. Issey, 1918, Thurston (K), 1945, Baker (Bak.); between Wades bridge and St. Minver, 1945, Baker (Bak.); Par, 1911, Druce (B.M., Ox., WNH). Recordfrom Polzeath (in Davey, Fl. Cornwall, 1909), and Gorran Haven (Reid 1911) are almost certainly correct.
 - S. DEVON: East Prawle, 1938, Chapple & Rob (K, Ox.); Brixham, 1931, C. I. & N. Y. Sandwith (K); between Babbacombe and Torquay, 1834, Borrer (K.Borr.); many stations around Torquay; Watcombe, 1914, Larter (Ex.Hiern); Drewsteignton, 1909, Hiern (Ex.Hiern); Hole's Hole, W. Bere Ferrers, 1871, Briggs (B.M.).
 - N. SOM.: Leigh Woods; Cheddar Gorge, 1918, Roper (L.Rop.), 1938, R. & K. Tuckins (B.M.); 1945, Baker (Bak.).
 - DORSET: Pumfield, near Swanage, 1882, Ridley & Fawcett (B.M.); near Swanage, 1884, Murray (B.M.) (probably the same station).
 - W. SUSSEX: Cockbush Common, 1833, G. E. Smith (Cam.); Clymping (Middleton), 1930, Lousley (Cam.).
 - W. GLOS.: Observatory Hill, Clifton (St. Vincent's Rocks), 1924, Roper (B.M., K, Cam., WNH, L.Rop.), 1953, Townsend (Towns.).
 - 44. CARM.: near Newcastle Emlyn, 1934, Chapple & Parry (Ox.).
 - H. 4. MID CORK: Cork, 1848, Carroll (B.M.).
 - 6. WATERFORD: Dungarvan, 1881, Britten (B.M.), Britten & Nicholson (B.M., Camb., Ox.).

Fig. 2 shows the distribution in map form. This account of the distribution of this subspecies is far more complete than that given by Wilmott (1921) and differs considerably from the overall picture presented by Druce (1932) and Warburg (1952). These differences and the many incorrect references to be found in local floras are due to the extensive confusion which existed in the older literature between G. purpureum Vill. and the prostrate maritime race of G. robertianum (which was frequently miscalled G. purpureum by British authors prior to 1921 and occasionally since). The originator of this misconception in Britain appears to have been Syme (1864). The confusion has been increased by a beautiful photograph of prostrate G. robertianum growing on shingle near Rye, Sussex, which appears in Sir Arthur Tansley's great work (1939) with the statement that "Geranium purpureum Vill. is a characteristic species of the south-eastern shingle beaches."

The earliest Sussex record of G. purpureum subsp. purpureum is from Cockbush Common on the west side of Chichester harbour. As pointed out by Wolley-Dod (1937) "Cooper (1834) gives a short description of it at Cockbush and Middleton (i.e. Clymping Sands) indicating that he found the true species there." However, we do not need only to trust Cooper's judgment, for through the years there have existed unnoticed four small specimens collected on June 3, 1833 by the Rev. G. E. Smith. At one time these plants rested in the Henslow Herbarium and they now form part of the Cambridge University collection. They were collected at the same time as prostrate maritime G. robertianum and were mounted on the same sheet. Their true nature was appreciated for the sheet is labelled "Geranium robertianum with G. purpureum. Cockbush Common. Sussex." In view of the fact that no subsequent collection had been made in this storm-damaged area, it is to be feared that the population is now extinct.

A rather similar story attaches to the other West Sussex record. In this case, erect specimens were collected in 1930 on shingle at Clymping (Middleton) between Little-hampton and Bognor at the station for the prostrate subsp. forsteri (see p. 000) by Mr. J. E. Lousley. Some of the specimens which were distributed give the impression of having grown upright in shade and, when I visited the population between 1945 and 1948 only plants shaded by concrete blocks or the wooden groyne were found growing erect. Nevertheless, Mr. O. Buckle (in litt.) tells me that he knows of a small population of G. purpureum with an ascending habit growing near Clymping so, until tests are made on these plants in culture, the record must be taken as correct.

Subsp. purpureum appears to be absent from Hampshire and very rare in Dorset, despite the first record for England at Swanage (see Wilmott, 1921), but begins to be locally common in South Devon. Many of the numerous localities given by Martin and Fraser (1939) are, however, incorrect, and the species occurs in only four areas, all but one of them coastal. The exception is Hiern's specimen from Drewsteignton. All records from North Devon are erroneous. The Cornish populations are all relatively well-known and this subspecies is probably more common around Newquay and by the estuary of the River Camel than elsewhere in England.

The erroneous records by E. S. Marshall and others having been discounted, it seemed for a long time that the only Somerset station was in Leigh Woods. Here the species was first seen growing under a wall by Miss A. Carpenter in 1837 whose specimen of a shade form is at Cambridge. It was first recognised, cultivated and commented upon by Moss (1912) and, since then has been repeatedly distributed, by J. W. White and others. Whether this has contributed to its apparently decreased numbers is problematical.

A record for Cheddar Gorge by H. M. Drummond-Hay was backed by a specimen collected in 1871 and lodged in the Boswell-Syme collection at the British Museum

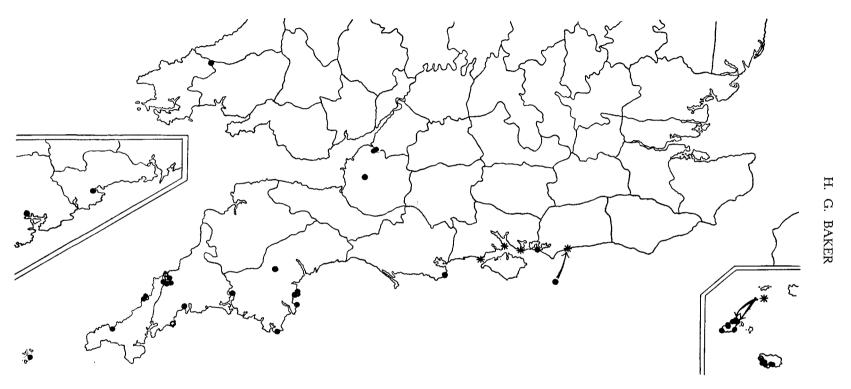


Fig. 2. Distribution of subsp. purpureum ● (O where specimen not seen) and subsp. forsteri ★ in the southern vice-counties of England and Wales (Southern Ireland and the Channel Isles inset).

(Natural History). It is quoted by White (1912). As expected, it proved, on examination, to be G. robertianum, of which several forms occur at Cheddar. However, genuine specimens of G. purpureum subsp. purpureum were collected by Miss Roper in 1918 and by R. and K. Tuckins in 1938; they do not appear to have been recorded in the literature. In 1945 I collected the plant growing on a ledge on the south side of the Gorge (and have used this material in experimental studies) and, in 1946, saw the species again growing on the roof of a greengrocers' stall in the Gorge (where seed had evidently dropped from the cliffs above). Interested by this, Mr. N. Y. Sandwith kept a look-out for the species and confirmed its presence.

The single station in Gloucestershire lies across the Avon Gorge from Leigh Woods. G. purpureum was first recognised on Clifton Down as recently as 1925 by C. Wall. Herbarium specimens suggest that this population has suffered some introgression from G. robertianum. This also applies to the relatively recent Carmarthenshire record, for, although it is referable to G. purpureum, the single specimen from Newcastle Emlyn has several features reminiscent of G. robertianum. A population-analysis in this locality might be very rewarding particularly as this is a remarkably disjunct outpost for G. purpureum. Similar suggestions of interspecific hybridisation apply in the Torquay area, at Bere Ferrers, and in north Cornwall.

Druce (1932) is in error in including the Isle of Wight and Breconshire in the range of G. purpureum.

Of the records from outside England and Wales, those from the Channel Isles are, in general, well known. The record from Bordeaux Harbour is of interest in that subsp. purpureum occurs there at the same station as the subsp. forsteri and, apparently, in circumstances reminiscent of those at Clymping, Sussex. The two Irish records are of long standing and are quite genuine although, surprisingly, they are not given by Druce (1932), nor by Praeger in any of his lists. At Dungarvan, however, there is a suggestion of natural hybridisation with G. robertianum. The records from Kerry, Clare and Galway (Moore & More, 1866; Colgan & Scully, 1898; Praeger, 1909, 1934a, 1934b; Scully, 1916; Warburg, 1952; Webb, 1952) are all due to confusion with prostrate maritime G. robertianum.

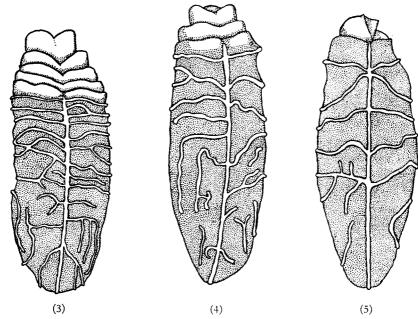
In the Scilly Isles, only G. robertianum is reported in the literature but Curnow's specimen in the National Museum of Wales appears to be G. purpureum. The literature records of G. robertianum (kindly supplied by Mr. J. E. Lousley) are all rather old and may also turn out to be referable to G. purpureum. Further collecting is very desirable.

- G. PURPUREUM subsp. FORSTERI (Wilmott) comb. nov.
 - G. purpureum Vill. sec. T. F. Forster (1830), Engl. Bot. Suppl., 3, 2648.
 - G. robertianum var. y Babington (1851), Man. Brit. Bot., ed. 3, 62.
 - G. robertianum var. purpureum (Vill.) sec. Syme, 1864, Engl. Bot., ed. 3, 2, 204.
 - G. purpureum var. forsteri Wilmott (1921), J. Bot., 59, 95.

Type locality: Clymping (Middleton), W. Sussex, England.

Plants of this subspecies have a prostrate habit, for the leader soon branches and the branches run at only a slight angle with the ground although the tips ascend. The petioles of the rosette leaves are still shorter than those of subsp. purpureum. They grow only in the stabilised area at the rear of certain shingle-beaches. In cultivation they flower about a fortnight later than British material of subsp. purpureum.

While the fruits of most British representatives of the subsp. purpureum are quite distinctly ridged, any population of subsp. forsteri shows a considerable range from typical purpureum to fruits very like those of G. robertianum (Figs. 3-5) and both glabrous and hairy fruits occur together. This makes the determination of herbarium material



Figs. 3-5. Dorsal views of three fruits from the population of subsp. forsteri at Clymping, W. Sussex (× 20), showing a transition from the typical purpureum pattern (left) to a robertianum pattern (right).

rather more difficult. There has been some doubt as to the correct name for this subspecies. Rouy (1897) describes his maritime G. purpureum Vill. var. littorale as having the petals "une fois plus longs que le calice." These petals (the measurement refers to the limb) are certainly large for G. purpureum and for this reason Wilmott (1921) dismisses the possibility that this represents the same taxon as his var. forsteri. This could not be regarded as the last word on the subject for whereas Wilmott concluded, quite unjustifiably, that the "rarement presque orangées" added to the "anthères jaunes" in the description of purpureum was "presumably added for the benefit of this G. Robertianum form" he admitted that he had seen no material from Rouy's type-locality (maritime shingle between Cayeux and le Hourdel, dept. Somme). Actually Rouy points out that it is in his var. semiglabrum that the anthers are rather orange.

However, there is material of Rouy's var. littorale at Kew from the classic locality and an examination of this sheet together with several other collections from the same population (in the Paris herbarium) shows unquestionably that it consists of the nearly glabrous prostrate maritime form of G. robertianum which was first described by Babington (1851) as var. maritimum. Consequently Wilmott's name var. forsteri is genuinely the first to have been given to prostrate G. purpureum.

The following stations for subsp. *forsteri* are represented in British herbaria:— CHANNEL ISLES:

- GUERNSEY: Bordeaux Harbour, 1892, Marquand & Groves (B.M.), 1902, Cooper (B.M.), 1912, 1914, Barton (B.M., Camb., Ox.); St. Sampson's Bay, 1894, Gray (Camb.); Fort Cumberland, 1876, Wright (B.M.); Fort Doyle, 1892, Miller (Camb.).
- V.c. 11. S. HANTS.: Stoke's Bay, 1829, Borrer (K.Borr., B.M.—Syntypes), 1871, Warner (B.M.Bosw.), 1878, 1883, J. Groves (B.M.); Southsea, 1836, E. P. (B.M.); Portsmouth, n.d., Macreight (K); Calshot, 1871, Streatfield (B.M., B.M.Bosw.); Hurst Castle, 1924, Turrill (K), 1928, 1929, Marsden-Jones (K), 1934, Ballard & Hubbard (K).
 - 13. W. SUSSEX: A pair of compact populations sampled by many collectors and variously referred to as at Clymping, Middleton, Atherington or simply "between Littlehampton and Bognor," type and syntypes, 1919, A. J. Wilmott (B.M.). Also an isolated plant "close up to the sandhills at Littlehampton," 1919, Wilmott (B.M.).

It is not certain how many separate stations were represented here, but it is virtually certain that subsp. *forsteri* has been extinguished by man's activities in its Hampshire stations with the exception of that at Hurst Castle. The Sussex populations are now very small. Wilmott (1921) discusses the possibility that this subspecies occurred at one time at Selsey (on the authority of Dillenius) and at Swanage, in Dorset (from a reference by Sherard), but no vouchers have ever been located.

The general impression given by the distribution and state of the populations of both subspecies is far from being one of expansion (as suggested by Reid, 1911). It is rather one of gradual diminution and, in the case of outlying populations, of approaching or actual extinction. Along the south coast a retraction westwards seems to be indicated while the headquarters remains in the West Country. If this be the case, subsp. forsteri has lingered longer than subsp. purpureum and their relative numbers at Clymping (before seaweed-clearing by tractor almost wiped them out) seem to substantiate the belief that subsp. forsteri finds the conditions less unfavourable than subsp. purpureum and is slower to disappear. On the other hand, the extreme localisation of this subspecies, to a group of stations in Sussex and Hampshire on the one hand, and Guernsey on the other, might suggest a separate origin for the subspecies in each. In speculating upon this it may not be without significance that subsp. purpureum and prostrate G. robertianum are both known to have occurred in relatively close proximity to these groups of the prostrate subsp. forsteri. A combination of the features of subsp. purpureum and prostrate G. robertianum could produce the characters of subsp. forsteri, both morphological and ecological (including an intermediate climatic tolerance).

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