

## The taxonomic treatment of polymorphic variation

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### ABSTRACT

The argument is advanced that polymorphic variation in many characters, e.g. flower-colour, hairiness, is common in British (and European) plants; that the extent of the polymorphism is often geographically variable; that it may be of evolutionary significance; and that it is sometimes worthy of taxonomic recognition, under the category of *forma*. Two new forms and a new varietal combination are recognised within *Viola riviniana* Reichenb.

The treatment of variation by taxonomists is not always consistent. For example, in an apomictic species such as *Rubus fruticosus* L. a single deviant individual in a population may be described as a new species, though it may be found only in a single locality and may possibly not be true-breeding. On the other hand, the white- and red-flowered variants of a species such as *Cirsium palustre* (L.) Scop. may not receive taxonomic recognition of any kind, even though the polymorphic variation which they show may be widespread and of considerable biological significance.

In the last 40 years, an increasing amount of interest has been taken, at first by zoologists, and then by botanists, in the kind of variation known as polymorphism, exemplified by the colour variants of *Cirsium palustre*, in which populations in the British Isles may consist of either variant or a mixture of the two in varying proportions. The interest has grown mainly among population geneticists and genecologists, rather than systematists. Good examples of this approach are to be found in the work of Crosby (1949) on the homostyle *Primula vulgaris* Huds. in southern England, and in the studies of Daday (1954) and Jones (1970) on polymorphism in cyanogenic glucosides in *Trifolium repens* L. and *Lotus corniculatus* L. respectively. It is interesting to note that in none of these species have the variants investigated been described taxonomically, and given a name. It is my contention that such taxonomic recognition should be given, preferably at the level of *forma*. I would suggest, for example, that the homostyle variant of *Primula vulgaris* and the cyanogenic variant of *Trifolium repens* should both be named and described. The genecologists themselves are usually not anxious to undertake a task of this kind, and it should become the duty of friendly systematists to persuade them to do so.

In the meantime, I should like in this brief paper to discuss one or two further examples from my own experience. These are intended to illustrate the interest and value of variation of a polymorphic nature, especially when viewed against a geographical background. The examples will also, I hope, support the case for taxonomic recognition.

The first example is that of variation in flower-colour in *Primula vulgaris*. In Britain, the yellow flower is universal, but here and there plants with white, red, pink or lilac flowers occur. They are mentioned in many of the older county Floras of southern England; and they are well known in Pembrokeshire, where populations containing plants with both pale lilac and yellow flowers

were early noted by Gray (1863), and have since been genetically investigated by Marsden-Jones & Turrill (1944). It is sometimes thought that these variants have come from gardens; but it is at least as likely that the plants have been moved in the opposite direction, i.e. from native habitats into gardens, and there is no reason to doubt that some at least are native. All the colour variants have been named, at one time or another (Wright Smith & Fletcher 1947), though the names are not widely quoted.

In the Balearic Islands, *P. vulgaris* occurs as subsp. *balearica* (Willk.) W. W. Sm. & Forrest, which has white flowers; it also differs from typical plants in other characters, such as the indumentum of the leaves. In Asia Minor, *P. vulgaris* occurs as subsp. *sibthorpii* (Hoffmanns.) W. W. Sm. & Forrest, and this differs in having red flowers and again in some other characters. And in an area by the Caspian Sea, there is yet another subspecies, subsp. *heterochroma* (Stapf) W. W. Sm. & Forrest, which is polymorphic for flower-colour, with white-, rose-, purple-, violet- and yellow-flowered plants mixed up in the populations.

The experiments of Chittenden (1928) showed that in *P. vulgaris* white flower-colour is recessive to yellow, only a single gene being involved; and although the white-flowered Balearic and Caspian plants have not been investigated, genetically, it is likely that their genetic basis is the same. Thus a variant which, looked at in Britain, appears to be a rare mutant, not mentioned in many Floras, is the only one which occurs in the Balearics and forms a significant component of the Caspian populations. This suggests that *P. vulgaris* has always shown a tendency to vary in flower-colour; and that the range of colours found in any particular region will vary, presumably in an adaptive way, from one region to another. In the case of the small and localised populations of the Balearics, it is possible that the white alleles have become fixed in the population, perhaps as a result of chance (Sewall Wright effect), and have persisted in isolation for a considerable time.

An interesting point also arises here as to exactly what is the adaptive significance of flower-colour in this species. Since the time of Darwin, there has been controversy over the nature and proportion of insects which pollinate the primrose (see, for example, the articles by Dallman (1921), Christy (1922) and Marsden-Jones (1926)), and this is an area in which further investigation is necessary. According to information given by Proctor & Yeo (1973), many insects do not distinguish sharply between yellow and white flowers, so that this form of variation may be adaptively more or less neutral.

My second example is concerned with a different kind of character, viz. indumentum; this is a character widely used in taxonomy, though its adaptive significance is frequently obscure. One kind of variant, found in *Viola riviniana* Reichenb., is the presence or absence of backwardly-directed hairs on the peduncle (the hairs are short and inconspicuous). A hairy variant of this kind is known in the literature as forma *villosa* Neum. and has been recognised in a number of Floras. It is probable that most populations in the British Isles have glabrous peduncles and that the hairy variant is rare; but hairy plants occur sporadically. In 45 collections from nature and from herbaria, it was found that 37 were glabrous, 6 hairy and 2 contained both glabrous and hairy plants. There are indications that western European plants in general vary in a similar way. Presence of hairs does not appear to be correlated with any other character in this very variable species; and it has been shown experimentally that the

character is controlled by a single gene, with hairiness dominant to glabrousness, and segregating in a disomic fashion (24:9,  $\chi^2 = 0.096$ ,  $p < 0.01$ ) in the  $F_2$ . The species is an allotetraploid; in crosses with the diploid, glabrous species *V. reichenbachiana* Jord., hairiness is again dominant.

Another diploid species allied to *V. riviniana* is *V. rupestris* F. W. Schmidt; and in western and central Europe this species is predominantly hairy, though this time the hairs are found not only on the peduncle, but on the capsule, the calyx and the petiole. In crosses with glabrous *V. riviniana*, hairiness is again dominant, though because the hybrid is sterile the genetics cannot be worked out. As in *V. riviniana*, *V. rupestris* shows variation in hairiness, and a var. *glabrescens* (Neum.) W. Becker and a var. *glaberrima* Murb. have been described. Within the range of *V. rupestris*, in lowland western and central Europe, these variants are rare, i.e. the situation is the reverse of that in *V. riviniana*. Experiments have shown that some hairy, glabrescent and glabrous plants of *V. rupestris* breed true (Valentine & Harvey 1961), but the genetics have not been investigated by inter-population crosses. In parts of Scandinavia, Jälas (1950) has shown that var. *glaberrima* becomes commoner and may be the main component of the population; the same is apparently true of subalpine populations in central Europe.

*V. adunca* Sm. is a North American species, with diploid and tetraploid races (McPherson & Packer 1974), which is closely related to *V. rupestris* and which may be regarded as a vicariant of it. It also shows a parallel variation in indumentum. In a series of collections from the herbarium of the University of Montreal (MT), from 17 localities in the province of Quebec, 11 had a hairy peduncle, 4 a glabrous peduncle, and 2 included plants with both glabrous and hairy peduncles. Again, the hairy variant is commoner than the glabrous, and this has been confirmed by field observations. On the other hand, the closely allied diploid species *V. labradorica* Schrank, which differs from *V. adunca* in leaf-shape and a more northerly geographical distribution, is uniformly glabrous.

It is of course by no means certain that the gene concerned with the hairy/glabrous character is the same throughout all these species, though it is reasonable to suppose that it is. If so, it is interesting to see how the frequency of the alleles may vary from species to species, with sometimes the glabrous and sometimes the hairy variant being the more abundant. Seen in this light, the obscure character of 'hairy peduncle' in *V. riviniana* takes on a new significance; it becomes worthy of study, hence of careful recording, and hence of naming. So far as I know, the variants in *V. adunca* are not named.

Another problem which comes to mind, and which can only be touched on here, is that of the adaptive significance of the presence or absence of hairs on the peduncle. In a recent review Levin (1973) quoted work on agricultural plants which demonstrates a negative correlation between hairiness of leaves and the resistance of the plants to attack by phytophagous insects, and this is suggestive of a causal relation. Whether this kind of system operates in *Viola* we have no idea. Intraspecific variation in indumentum correlated with variation in habitat or location is well known in many species, as for example in the lowland and upland ecotypes of *Potentilla glandulosa* Lindl. (Clausen, Keck & Hiesey 1940), but again the adaptive significance of this has not been studied.

I have tried, with these two examples, to show that apparently minor variation in one part of the range of a species may prove to have significance in other parts of the range of that species, or in another allied species; and it is likely that there

are many similar cases waiting to be investigated. I would therefore suggest that taxonomists in general, and British taxonomists in particular, should become a little more conscious of variants of the kind I have been describing, and should be prepared to take the risk of giving them a name, in the category of *forma*. In the last three years, I have been on the look-out, during occasional field excursions, for colour variants of common plants; and I have found and photographed six, in *Erica tetralix* L., *Ononis spinosa* L., *Epilobium angustifolium* L., *Centaurium erythraea* Rafn, *Digitalis purpurea* L. and *Petasites hybridus* (L.) Gaertn., Meyer & Scherb. In the first five of these, the less common variant had white flowers, and in four of them the normal and white-flowered variants occurred together in the same population. In the case of the *Petasites*, the less common variant was nearly white in colour, both the involucre bracts and the bracts of the main peduncle being affected. I have not yet made a thorough search of the literature to find if the albino variants have been described taxonomically, though I know that some of them (e.g. the white variant of *Erica tetralix*) are mentioned in several Floras as a part of the description of the species. My case for recognising them rests, as I have indicated, on their potentiality for polymorphism. In his important paper on the subject, Huxley (1955), following Ford (1940), defined polymorphism (or morphism as he called it) as a state 'in which (usually sharply distinct) genetic variants or morphs coexist in temporary or permanent balance within a single interbreeding population in a single spatial region, and in such frequencies that the rarer cannot be due solely to mutation, or to the spread of selectively neutral mutants.' As I have suggested in the case of the white-flowered variant of *Primula vulgaris*, a rare variant ascribable to occasional mutation in one area, such as white flowers in Britain, may become a frequent or even a dominant variant in other areas. It is thus important as part of the raw material of evolution on which selection may work here and there; and collection of information about it may be useful, and may even draw attention to polymorphic situations that had not been suspected. It could well be that the albino variants of the six species which I have mentioned above may be part of a polymorphism somewhere in their range. I do not know; but if they are named—and naming is the most important step towards recording them and getting them into the literature—then there is a chance of making a discovery.

In the *International Code of Botanical Nomenclature*, a series of categories, such as subspecies, variety and *forma*, is listed as available for the description of infraspecific variation. In some quarters, in both the British Isles and North America, there is a tendency to use only the subspecific category and to dismiss more minor variation as trivial and not worth recording. When genecological studies are made, the variants are utilised and their evolutionary significance is assessed, but then, like under-sized fish, they are often thrown back into the pond, to swim away and thus to be lost to the general botanist, who cannot find them in his Flora because they have no name. In the tropics, where primary survey is still the main object, this attitude is understandable; but in the much-studied north temperate region it seems to me to be wrong-headed and wasteful.

In conclusion, I should like to remedy an omission of my own. I have had occasion to describe another variant in *Viola riviniana*, which is concerned with the ability of the plant to propagate itself vegetatively by the production of adventitious shoots (soboles) from the roots. This is a character which varies polymorphically in British populations and is correlated with the possession of



supernumerary chromosomes. I regret to say that it has not been named, and accordingly I now propose names, to go with (a) var. *riviniana* and (b) var. *minor*.

a) *Viola riviniana* Reichenb. var. *riviniana* forma **prolifera** Valentine **forma nov.**

A forma *riviniana* radicibus surculos vegetativos emittentibus, chromosomatibus plus quam 40, usque ad 47, differt.

Differs from forma *riviniana* in being soboliferous, i.e. in producing buds on the roots which develop into leafy shoots and serve as a means of vegetative reproduction, and in having supernumerary chromosomes, up to 7 in number (forma *riviniana* has  $2n = 40$ ).

HOLOTYPE: Light wood and leaf mould, Deepdene grounds, Dorking, Surrey, v.c. 17, 13/5/1917, A. J. Wilmott, **BM**  
(Illustrated in Valentine (1949))

b) *Viola riviniana* Reichenb. var. **minor** (Murbeck ex E. S. Gregory) Valentine, **comb. et stat. nov.**

*V. riviniana* forma *minor* Murbeck ex E. S. Gregory, British Violets, 63 (1912)

As stated in *Flora Europaea* (Valentine *et alii* 1968), I now prefer to treat this taxon as a variety rather than as a subspecies.

Forma **sobolifera** Valentine, **forma nov.**

A var. *minor* forma *minor* radicibus surculos vegetativos emittentibus, chromosomatibus plus quam 40, usque ad 47, differt.

Differs from var. *minor* forma *minor* in being soboliferous and in having supernumerary chromosomes, up to 7 in number (forma *minor* has  $2n = 40$ ).

HOLOTYPE: Mossy turf in peaty soil, summit of Cronkley Fell, N.W. Yorks., v.c. 65, 18/5/1949, D. H. Valentine, **MANCH**

Forma *prolifera* and forma *sobolifera* are fairly widespread in the British Isles. Forma *prolifera* has also been recorded from the Netherlands by Gadella (1963), and from Germany and Switzerland by Schmidt (1961). Both forms will probably be found in many parts of the range of the species. Both the soboliferous character and some of the supernumerary chromosomes may also be transmitted to interspecific hybrids; soboliferous natural hybrids are known with *V. reichenbachiana*, *V. rupestris*, *V. lactea* and *V. canina*. A plant of *V. reichenbachiana*  $\times$  *V. riviniana*, with many leafy shoots springing from the roots, is illustrated in Valentine (1949), and a general account of the polymorphism is given in Valentine (1956).

Huxley's definition of polymorphism implies that the difference between the morphs is of an adaptive nature and under the influence of natural selection. This point, to which reference has briefly been made in the discussion of flower-colour in *Primula vulgaris* and of indumentum in the *Viola* species, is one of considerable evolutionary interest, though often very difficult to investigate. The alleles controlling the soboliferous character are dominant; and the fact that the character facilitates vegetative reproduction might lead one to think it would spread rapidly in natural populations. Yet in many populations the character occurs only sporadically and, though it is widespread, it does not appear to be particularly common. There is probably here a state of balance

between the morphs, characteristic of polymorphic situations, and it would be interesting to know how it operates. It would be especially useful to know how plants of the morphs compete under field conditions, and whether their reproductive capacity by seed differs.

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