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Variation in Leaf Pubescence in *Viola incognita* Brainerd and *V. renifolia* Gray

By NORMAN H. RUSSELL

One of several morphological characters widely used in the separation of species and varieties in the genus *Viola* is that of lamina pubescence. In some cases, particularly in the common acaulescent* blue violets, specific distinctions based primarily on leaf pubescence have proven unsatisfactory. In other instances in *Viola*, presence or absence of pubescence has served as an excellent separating character between certain closely allied species. In his comprehensive survey of hybridism in the violets, Brainerd (1924) often used the amount of pubescence as an indication of degree of hybridization and demonstrated in many cases that it was inherited apparently in Mendelian fashion. However, his results seem to indicate, on re-examination, that pubescence is inherited in a "quantitative" fashion. Amount of lamina pubescence apparently depends in most cases on several or many alleles.

Only rarely in the genus have the actual nature of the pubescence and its distribution on the leaf been observed or described. In certain of the white violets, to be discussed below, position and type of pubescence are important diagnostic characters, and both are almost certainly inherited.

For a number of years the author has studied morphological variation in the acaulescent, white-flowered violets. There are six species of these violets which belong to the group *Stolonosae* of the subsection *Plagiostigma* of *Viola* (Russell, 1945). Among other things, lamina pubescence has been analyzed for all six of the violets; in five species variation in leaf pubescence has accounted for the erection of varieties or subspecies. The present study deals with two species, *Viola incognita* and *V. renifolia*, where the separation of varieties based on pubescence variation alone is thought to be inadvisable.

Part of the data presented below is taken from a thesis presented by the author in partial fulfilment of the requirements for the Ph.D. at the University of Minnesota. Acquisition of the population samples from New York was made possible by the generosity of

*"Acaulescent" is defined here as meaning plants with the stem almost completely below the surface of the soil.

the Directors of the Edmund Niles Huyck Preserve, Rensselaerville, New York, and a grant from them has financed preparation of much of the tabular material.

METHODS

In acquiring data regarding lamina pubescence variation, both ordinary herbarium specimens and population samples have been used. Measurements have been made on the sampled material either before or after pressing. In every case, all the leaves of each plant used were examined and those with the greatest amount of pubescence, in case of variation on the same rhizome, were used as standards. Variation of this type is not common; though it may be true in some genera, in *Viola* there is apparently very little loss of trichomes as the leaf ages. It was noted, however, that there may be some difference in amount and pattern of pubescence on the "immature" leaves of early spring and the "mature" leaves of late spring and summer. In these studies juvenile or early spring leaves were not considered.

Pubescence was observed in four areas on the leaf: the upper and lower surfaces of the lamina, the lamina margins, and the petiole. Amount of hairiness was estimated and arbitrary scales were set up. On both upper and lower leaf blade surfaces a value of zero (0) indicated absolute glabrousness, or fewer than five hairs on the whole surface. A value of one (1) indicated a few hairs on the major veins. If not only the veins but also the inter-vein surfaces of a part of the leaf were hairy, the score of two (2) was given, and finally, a score of three (3) was assigned if the surface was uniformly hairy. On the lamina margin a score of zero indicated a lack of hairs, a score of 1 a fringe of hairs covering at least half the leaf perimeter. The petiole was scored as 0 if glabrous, 1 if pubescent.

No observations or measurements on the length or general morphological character of the hairs in the four areas were recorded, though differences were noted. For example, the lamina margin hairs are generally short and stiff, regardless of the nature of the blade surface hairs. The type of pubescence differs slightly between the two species, the hairs of *V. renifolia* being generally weaker and somewhat intertwined, whereas those of *V. incognita* are usually erect and not at all or very rarely intertwined.

Pubescence has been analyzed in two principal ways. In the first method, which has been found more satisfactory, four classes were recognized with respect to lamina pubescence: upper surface only

hairy, lower surface only hairy, both surfaces hairy, and both surfaces glabrous. In the Tables, these are referred to as lamina pubescence classes 1, 2, 3, and 4, respectively. A score of 1, 2, or 3 indicated hairiness, of 0 the glabrous condition. The second method (Figure 4) has been used in the analysis of herbarium material. Here, instead of four classes, a total of 66 have been recognized. These represent all the possible combinations of the total of 12 possible scores for the four areas.

RESULTS

Viola incognita Brainerd

V. incognita is a small, inconspicuous violet, commonly found in rich, moist woods, composed either entirely of deciduous trees or of a mixture of deciduous and evergreen trees. It is frequent under beech-maple, basswood-maple, beech-hemlock, and similar canopies. Where found it is often abundant, reproducing most effectively by long, leafy stolons. It is distinguished from other species of stemless, white violets by several features; the lower lateral petals are bearded, the cleistogamous capsules are purple or purple-spotted, and the leaves are virtually always pubescent to some degree. In these last two features it closely resembles *V. renifolia*, from which it differs most markedly in leaf shape (cordate as opposed to reniform) and the presence of vegetative stolons, which are absent in *V. renifolia*. The white violets are frequently difficult to distinguish; no single character will suffice, and a combination of them must often be used. However, there seems to be no doubt regarding the authenticity of the six species.

Brainerd (1905) in his original description of *Viola incognita* stated: "Peduncles, petioles, and lower surface of leaves pubescent with soft white hairs especially when young, the upper leaf-surface glabrous or nearly so; . . .". Later (1911) he described the variety *Forbesii* as follows: "Nearly or quite glabrous, except often for scattered white hairs on the upper leaf surface; otherwise like the type." Brainerd did not further modify the above descriptions in his work on North American violets (1921), and Fernald (1950) followed them. In none of the publications were characters other than this single pubescence difference used in separating the species and variety. Furthermore, both Brainerd and Fernald give the ranges of the two as overlapping throughout northeastern North America. Brainerd (1911) mentions that the variety seems to be found in more moist places, but no further differences are noted. A point worthy of mention is that the pubescence form attributed

to the variety *Forbesii* is almost identical with that found in a closely related species of violet, *V. blanda* Willd.

In Figure 1, the range of *V. incognita* is plotted from the herbarium specimens observed. Acknowledgments to the herbaria involved are made in another paper (Russell, 1954). Each dot represents an actual specimen or collection seen. In Figure 2 variation in one of the pubescence classes (lamina pubescent on the upper surface only) is demonstrated. This map was prepared by dividing North America into square areas, 100 miles on a side, and averaging measurements from all specimens seen in each square. Then phenocontours were drawn through means of equal value. This method will be explained in greater detail in a subsequent paper.

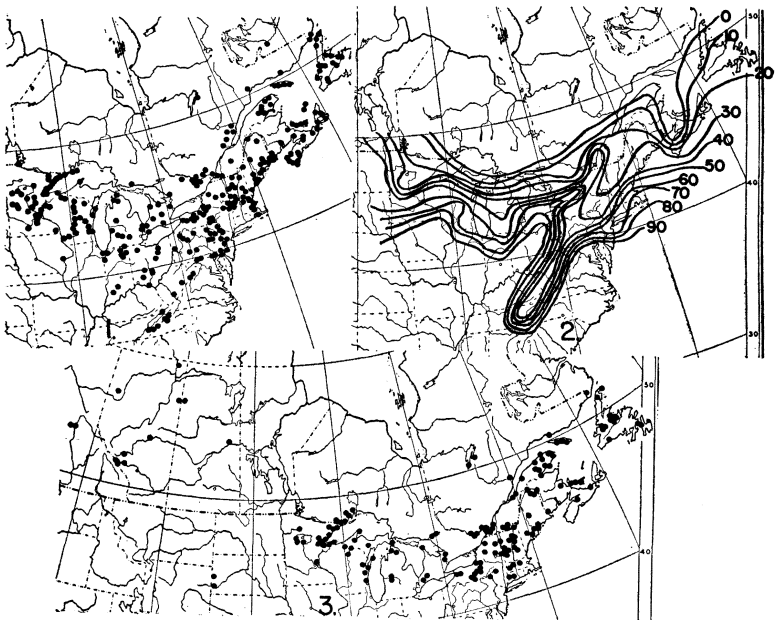


Figure 1. Natural distribution of *Viola incognita* Brainerd.
 Figure 2. The percentage distribution of lamina pubescence type one throughout the range of *V. incognita*. Further explanation in text. Figure 3. Natural distribution of *Viola renifolia* Gray.

Only for this particular distribution of lamina pubescence (Class 1) was it possible to construct a contour map. The other three classes (pubescent below, on both surfaces, and on neither surface) varied in a haphazard fashion. Figure 2 indicates that the pubescence type characteristic of the variety *Forbesii* is relatively more abundant in the southern part of the range, but still occurs in all but the very northernmost reaches of the range. Furthermore, it

was found impossible to correlate pubescence variation with any of the dozen other characters measured.

When the 66 individual classes of total leaf pubescence are considered, the distribution shown in Figure 4 is derived. Thirty-one, or almost half, of the total number of classes were represented in specimens examined from the Gray Herbarium. Further studies of material from other major herbaria, not indicated on the graph,

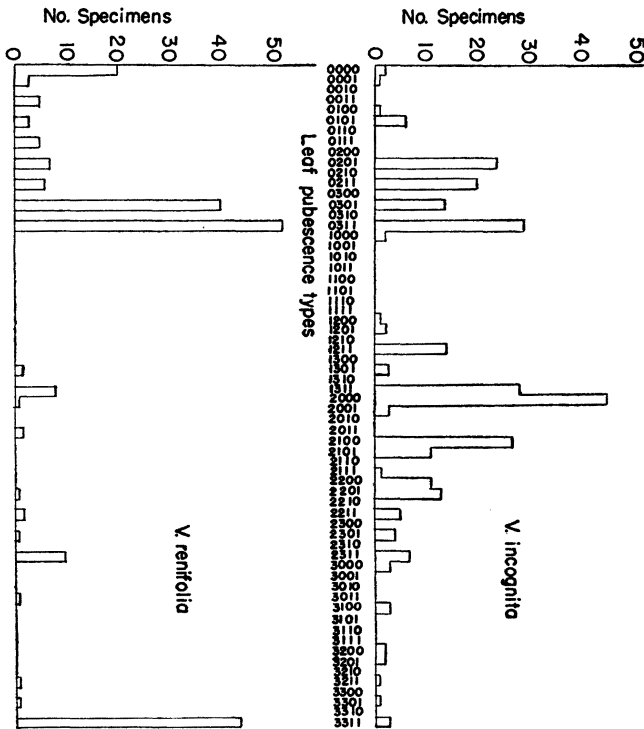


Figure 4. Distribution of the Gray Herbarium specimens of *Viola incognita* and *V. renifolia* among the 66 possible leaf pubescence classes. Each class or type has four numbers; the first refers to the upper surface of the blade, the second to the lower surface, the third to the margin, and the fourth to the petiole.

have increased this total considerably. It should be noted here that the two largest classes, 2000 (lamina pubescent above only, margin and petiole glabrous) and 0311 (lamina pubescent below only, margin and petiole pubescent), correspond to the species and variety as characterized by Brainerd.

Population samples have been taken and analyzed from two regions for both *V. incognita* and *V. renifolia*. In Table 1, the distribution of the specimens among the four major lamina pubescence types is indicated for one group of population samples.

These collections were all made in Minnesota except the last, which was made in western Wisconsin, about 40 miles northeast of Minneapolis. The first four samples were taken between Duluth and Grand Portage on the north shore of Lake Superior. The last four listed were taken in the vicinity of Minneapolis. The collection labeled "GBO-1" was made by Dr. Gerald B. Ownbey of the University of Minnesota; all others were made by the present author.

Table 1

Distribution of lamina pubescence types in population samples of *V. incognita* from Minnesota and Wisconsin. For key to types see text.

Collection	Number specimens	(types)			
		1	2	3	4
GBO-1	32	0	31	1	0
NR 96483	50	0	16	34	0
NR 48-46	9	0	9	0	0
NR 6124912	48	0	21	27	0
NR 61749	64	51	0	12	1
VH 81248AW2	27	16	0	11	0
HL 8548AW	13	6	1	3	3
ARC 81548AW	11	7	0	4	0
Totals	254	80	78	92	4

In Minnesota, if these eight samples are indicative of actual conditions, there is a definite localization of the conditions typical of the species in the northern part of the state, and the variety in the more southern region about Minneapolis. The specimens in Type 3 (lamina pubescent on both surfaces), however, are more abundant than either of the first two classes. If names are given to plants based on pubescence variation alone, this class is equally deserving of a name.

During the summer of 1953, a total of twenty-six population samples of *V. incognita* were taken on and near the Edmund Niles Huyck Preserve near Rensselaerville, Albany County, New York. This is a 500-acre, private preserve, dedicated to the preservation of the native vegetation and fauna for biological field research and for the recreation of the people of Rensselaerville and vicinity. The data from these collections are presented in Table 2. A quick perusal will indicate the abundance of lamina pubescence type number 2 (pubescent on lower lamina surface only), the condition typical of the species. In only three collections, numbers 67, 97, and 118, were there more plants with leaves pubescent above only. In these latter cases a large number of specimens had leaves pub-

escent on both surfaces. A feature not indicated by the tabular data is the fact that in New York the collections containing many plants in class 1 were obtained from boggy locations.

Table 2

Distribution of lamina pubescence types in population samples of *V. incognita* from New York.

Collection	Number specimens	(types)			
		1	2	3	4
9	18	1	15	2	0
23	34	0	28	6	0
25	35	0	30	5	0
29	47	17	28	0	2
30	40	0	35	4	1
33	40	0	39	1	0
37	40	0	34	6	0
49	40	6	27	7	0
57	40	10	24	3	3
59	40	4	28	5	3
61	23	0	23	0	0
62	34	0	34	0	0
63	11	0	11	0	0
67	40	11	3	25	1
69	40	0	36	4	0
72	40	0	40	0	0
76	84	0	80	3	1
80	40	2	30	2	6
84	40	3	37	0	0
87	40	2	34	1	3
94	40	1	34	5	0
97	40	27	3	10	0
106	14	0	14	0	0
111	40	2	37	1	0
118	39	16	13	10	0
119	40	0	40	0	0

The data just presented indicate some differentiation in *Viola incognita* between types with leaves pubescent above only, leaves pubescent below only, and leaves pubescent on both surfaces. Only a few specimens were found with laminas completely glabrous. These last are suspected of being hybrids with *Viola macloskeyi* subsp. *pallens*, another common white violet (Russell, 1954b). A more refined analysis indicates that not only the surface pubescence itself but also its location on the violet leaf may be genetically determined. From an evolutionary standpoint, this might indicate that differentiation is proceeding actively, that two formerly well-separated entities are merging, or perhaps that introgression from a closely related species, *V. blanda*, is occurring. These hypotheses will be examined in more detail in another paper. From a taxonomic viewpoint, there is considerable doubt in the mind of the author that an entity differing from a species in a single character,

and in this neither differing markedly, nor occupying a separate range, deserves the rank of variety.

Viola renifolia A. Gray

In *Viola renifolia*, a species closely related to *V. incognita*, a similar taxonomic situation obtains. A variety (*Brainerdii*) has been constructed on pubescence characters of the leaves alone. *V. renifolia* resembles the preceding species in several ways but can usually be quickly distinguished by virtue of its reniform leaves. Though sometimes found with *V. incognita*, it grows best under conifers, both the hemlocks of New York, and the spruces, firs, cedars, etc., of the northern forest. It is seldom as abundant as *V. incognita*; as a consequence of its lack of vegetative stolons, it does not form extensive colonies.

Freely translated, Gray's original description (1870) reads "leaves reniform with both surfaces and petiole villous-pubescent; scape pubescent." The authority for the variety *Brainerdii* is M. L. Fernald. In the eighth edition of Gray's Manual (Fernald, 1950) it is described as having the "leaves glabrous or promptly glabrate and bright green above, glabrescent beneath, the petioles similarly glabrescent; peduncles and sepals glabrescent." The distinction is then clear—the species is hairy on all surfaces, the variety glabrous or "glabrescent" on all parts.

In Figure 3 the natural distribution of *V. renifolia* is indicated. It was found impossible to construct phenocontour maps for any of the four types of lamina pubescence in this species, as variation seemed completely haphazard. In Figure 4 the distribution of Gray Herbarium specimens according to the sixty-six specific leaf pubescence types is illustrated, and it is seen that there are *three* major types, as in *V. incognita*. In addition to the type with both surfaces pubescent (the species) and that with neither surface pubescent (the variety), there is a third type (0301 and 0311) with the *lower surface only* pubescent. Though twice as abundant as either of the other two types, this third type does not have a name! Obviously a neglect of duty!

Only four population samples are available from Minnesota, and the data from these are presented in Table 3. The first three samples are from northern Minnesota, the last (NR 61749) from the Cedar Creek Bog, about 40 miles north of Minneapolis. These data are insufficient to indicate general trends, but do indicate very wide variation in leaf pubescence in both northern and southern Minnesota.

Table 3

Distribution of lamina pubescence types in population samples of *V. renifolia* from Minnesota.

Collection	Number specimens	(types)			
		1	2	3	4
GBO-1	19	0	8	7	4
NR 96482	11	0	0	0	11
NR 95481	8	0	4	3	1
NR 61749	26	6	1	18	1
Totals	64	6	13	28	17

Finally, data from six collections made in or near Rensselaerville, New York (Albany Co.) may be considered (Table 4). The largest of these collections (No. 68) was taken from the north slope of Hunter Mountain, in the Catskills. In all these collections, the "unnamed" condition (pubescence on the lower leaf surface only) predominates. In none of them are plants with pubescence only on the upper surface found; this condition is extremely rare in *V. renifolia*.

Table 4

Distribution of lamina pubescence types in population samples of *V. renifolia* from New York.

Collection	Number specimens	(types)			
		1	2	3	4
27	7	0	7	0	0
32	27	0	16	10	1
68	40	0	40	0	0
78	9	0	7	0	2
81	15	0	7	6	2
88	16	0	15	1	0
Totals	114	0	92	17	5

It may be concluded, from the present data, that in *Viola renifolia* there is even less excuse for the separation of a sub-specific entity than in *V. incognita*. Not only was just a single character used, but there is no evidence of geographic separation of the two named forms. Finally, a third, unnamed form is more abundant throughout the species range than either of the named forms.

SUMMARY

The distribution of leaf pubescence variations in *Viola incognita* Brainerd and *V. renifolia* Gray has been illustrated from three sets of studies; over the total range of the two species, using herbarium specimens; from population samples from Minnesota and

western Wisconsin; and, finally, from a series of population samples from the Helderberg Plateau in eastern New York.

In the case of *V. incognita*, there is good evidence of the partial segregation of a pubescence type (leaves pubescent on the upper surface only) in the southern part of the range of the species. However, in spite of this segregation, doubt is cast on the advisability of recognizing the variety (*Forbesii*) based on a single morphological character. Correlation with other characters could not be demonstrated.

V. renifolia proved more interesting. In addition to a completely haphazard distribution of the two pubescence types supposedly characteristic for the species and its variety (*Brainerdii*), a third type that had not been recognized in the literature was even more abundant. It was concluded that recognition of the variety *Brainerdii* here was apparently very illogical.

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