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Norman H. Russell
Grinnell College

Jeanette Graham
Grinnell College

Midwestern Population Studies of *Viola papilionacea* Pursh

By Norman H. Russell and Jeanette Graham[1]

Since about 1900 nearly every taxonomist concerned with the violets nas referred to *Viola papilionacea* Pursh as the "common blue violet". Generally speaking, the blue violets of towns and cities especially have been referred to this species. In the major herbaria, the folders containing specimens labeled *Viola papilionacea* are frequently much larger than those for any other species of the genus. Its habitat has been reported to be "near dwellings", "roadsides", "dooryards", and "common in moist fields". Its range is reported to be "Mass. to Minn., s. to Ga. and Okla.", and it has been reported from other places well outside this area. Fernald, for example, reports it as occurring from "centr. Me. and s. Que. to N.D. and Wyo., s. beyond our limits." Popular writers, when they list scientific names at all, usually choose *V. papilionacea* for their blue violet illustration.

In spite of such popularity, taxonomists have had much difficulty in defining this violet, or at least in applying their definitions to collected material. Every characteristic used to distinguish it can be found in its relatives. Considerable variation has been noted. For example, though it is said to be characteristically glabrous, the majority of herbarium specimens seen have had at least sparse pubescence. Flower color varies from pure white to dark blue. Leaf shape on named specimens is quite variable for the blue violets. This variation has rendered determination of many violet specimens extremely difficult, for *V. papilionacea* has a number of close relatives which, though apparently "good" species, have very similar leaf morphology to it. The closest of these is *V. sororia* Willd., and authors have tended to attribute much of the difficulty in distinguishing *V. papilionacea* to its apparent frequent hybridization with *V. sororia*.

Studies of the stemless blue violets of the midwestern states have been in progress by the senior author for the past two years and have involved morphological and ecological studies of population samples taken in Minnesota, Iowa, Nebraska, Missouri, Wisconsin, southern Michigan, and Indiana, and, in addition, studies of herbarium material and population samples from selected other states. Prior to the initiation of this research, other studies in the midwest had

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indicated that *V. papilionacea* might not be so common as had been thought. In the summers of 1956 and 1957 an effort was made to locate undisturbed (by hybridization) populations of *V. papilionacea.* As the data to follow indicate, not only were these rarely found, but disturbed populations also were rare—only thirteen being sampled in two summers' collecting. It is the opinion of the authors that the common blue violet is actually *Viola sororia,* and that *V. papilionacea* is a rather infrequent weed.

The thirteen collections of *Viola papilionacea* were made during the summers of 1956 and 1957. About half of these grew on railroad roadbeds, in ash and gravel, and the remainder in various other locations, all with a high degree of habitat disturbance. The geographic locations of these collections are indicated in Figure 1. The size of these samples varied from ten to fifty plants, depending upon the

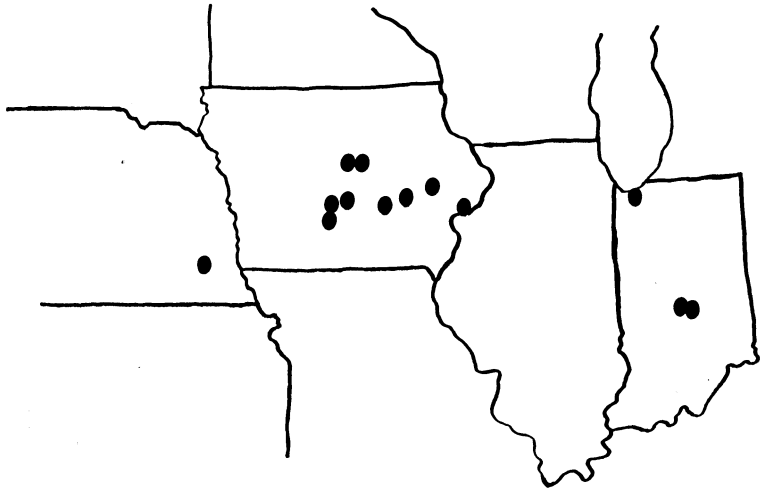


Figure 1. Locations of the thirteen population samples of *V. papilionacea.*

size of the actual populations. Within a population, specimens closer together than about ten feet were not collected because of the danger of obtaining members of the same clone. Generally, the populations sampled were quite small, consisting of only about one hundred or a few hundred plants.

A single, mature, undamaged leaf was taken from each plant and pressed and dried for later study. As all the collections were made in early summer, after petaliferous flowering had been completed, many completely developed leaves were available on healthy plants, and the largest of them was always taken.

These leaves were later subjected to a series of measurements to determine intra-population and inter-population variation. These

measurements have been discussed in considerable detail in other publications (Russell, 1952, 1956). Briefly, the measurements made were of lamina length (along the midrib), lamina breadth, an angle measuring the divergence of the apical margin from the horizontal ("apical angle"), the number of teeth (crenations) along one half of the leaf margin, pubescence on the upper lamina surface, the lower lamina surface, the lamina margin, and the petiole. For the upper and lower lamina surfaces, a score of 0 indicated a completely glabrous blade, of 1, a few hairs on the veins, of 2, hairs on the veins and also on some inter-vein surface, and of 3, many hairs completely over the surface. For the margin and petiole, a score of 0 indicated glabrousness, of 1, pubescence. Ratios were prepared between length and breadth of the lamina and between the length of the lamina and the distance from the leaf apex to one of the basal lobes ("1/11 ratio"). In addition, a figure representing "total pubescence" was obtained by adding the pubescence values from each of the four areas. Previous studies of a variety of violet species had indicated that leaf shape, vesture, and the number of teeth were little affected by environmental factors and hence would give a fair picture of genetic variation.

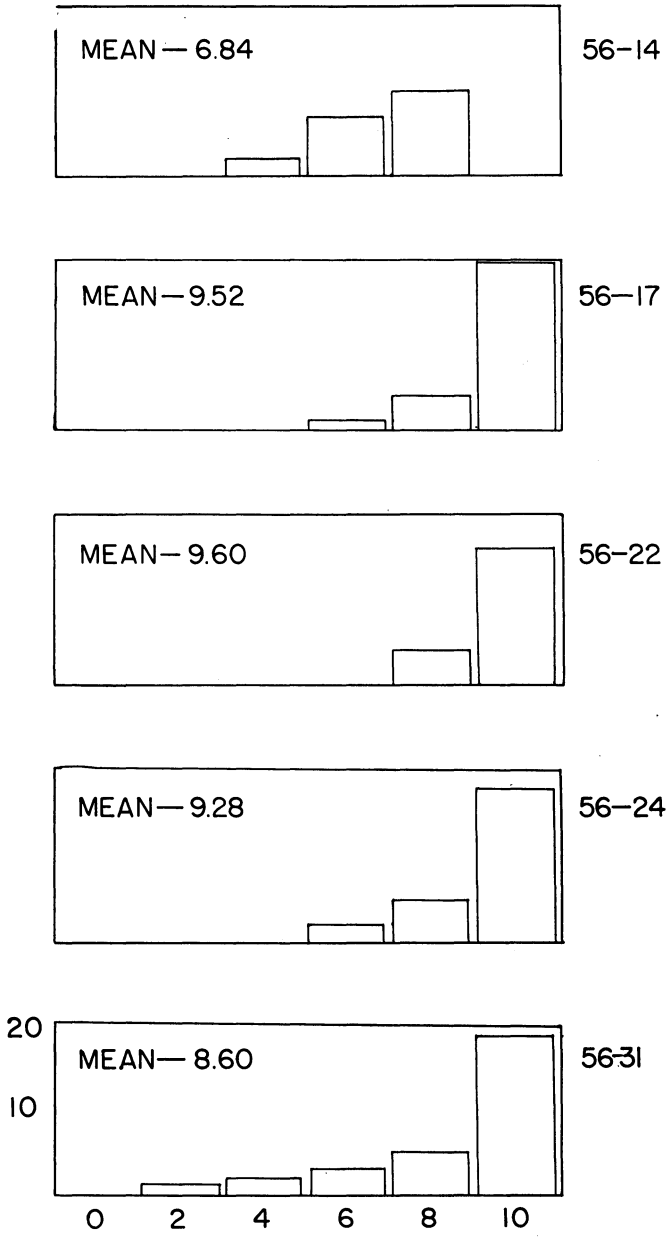
Table 1 represents a summary of the measured or computed characteristics of the thirteen population samples. In every characteristic a relatively large amount of variation was found. Compared with analyses of other violets (Russell, 1952, 1958, Russell and Cooperrider, 1955), *V. papilionacea* was indeed difficult to characterize morphologically. The authors believe this variability to be due in large part to hybridization with other blue violets, principally *V. sororia,* a very common species which frequently grows as a weed in towns and disturbed habitats and comes into close contact with *V. papilionacea.* To test this hypothesis, a type of hybridization index was prepared.

The hybridization index is a tool originally described by E. Anderson (see 1949) to indicate the extent of introgression between hybridizing species. It requires the use of a number of discrete characteristics; Anderson has suggested that seven different characteristics will almost completely eliminate the element of chance in the event of correlation of these characters. In the present study, a hybridization index was set up by the junior author, testing nine of the populations. Extremes of characteristics most like those usually attributed to *V. papilionacea* were given a value of 2 and those most different from the (hypothetical) *V. papilionacea* a value of 0. Then each plant of each population was scored for each of the five characteristics used. Therefore a plant (represented by a single leaf) that was like *V. papilionacea* in every character would have a score of ten and one unlike it in every way a score of zero.

Table 1

A Summary of the Characteristics of Thirteen Populations of *Viola papilionacea*

Sample Number	No. Spec.	Lamina length	L/b ratio	L/11 ratio	Apical angle	Number teeth	Pubescence above	Pubescence below	Pubescence margin	Pubescence petiole	Total Pubesc.
56-14	19	36.6 mm	1.14	0.81	75.5°		0.16	0.21	0.11	0.11	0.58
56-17	25	50.2	0.87	0.75	74.2		0.00	0.00	0.00	0.00	0.00
56-22	20	39.9	0.86	0.74	71.7		0.00	0.00	0.00	0.00	0.00
56-24	25	59.0	0.92	0.75	73.4		0.12	0.20	0.12	0.24	0.68
56-31	30	34.0	0.83	0.73	75.4		0.53	0.40	0.43	0.17	1.53
56-46	25	57.5	0.78	0.72	74.8		1.20	1.16	0.80	0.56	4.72
56-49	25	72.7	0.80	0.78	73.1		1.04	0.40	0.64	0.32	2.40
56-77	25	38.9	1.01	0.78	74.9		0.04	0.00	0.00	0.00	0.04
56-93	25	61.5	0.81	0.69	67.9		2.00	2.04	0.72	0.72	5.48
57-15	46	52.5	0.79	0.75		32.9	0.00	0.00	0.00	0.00	0.00
56-127	50	60.9	0.88	0.77		28.9	0.08	0.10	0.04	0.04	0.25
56-128	20	62.8	0.83	0.75		32.5	0.00	0.05	0.05	0.05	0.15
56-72	10	55.0	0.89	0.75		29.6	0.00	0.00	0.00	0.00	0.00
Means	345	52.4	0.88	0.75	73.3°	31.0	0.40	0.35	0.22	0.17	1.14


MEAN — 6.84
56–14
MEAN — 9.52
56–17
MEAN — 9.60
56–22
MEAN — 9.28
56–24
20
10
MEAN — 8.60
56-31
0
2
4
6
8
10

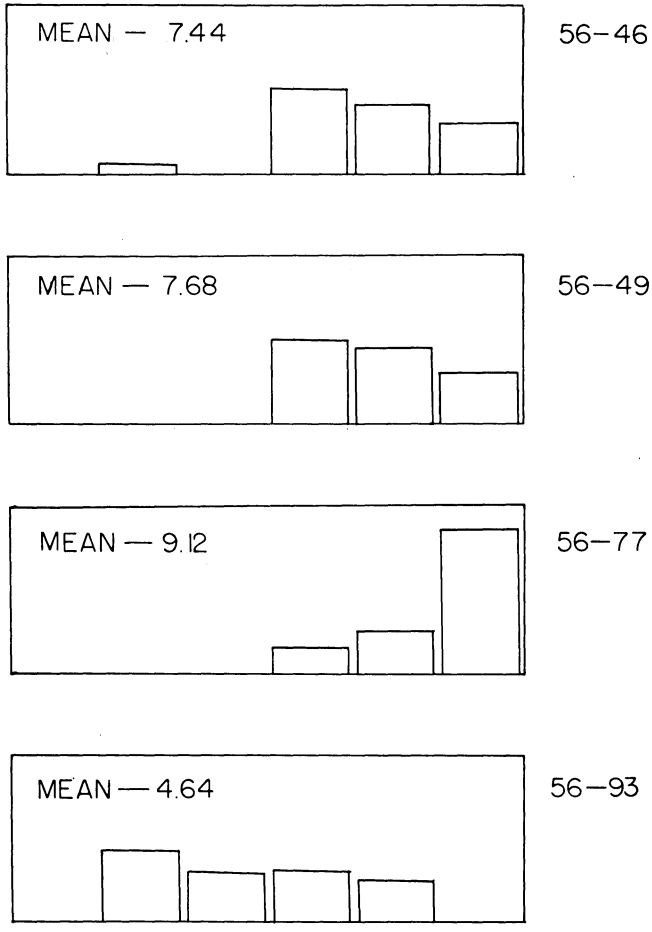


Figure 2. Bar diagrams illustrating the distribution of hybrid indices for nine of the thirteen population samples. A score of ten indicates a "pure" plant of *V. papilionacea*, while a score of zero indicates a plant that differs from *V. papilionacea* in all five characteristics

Characteristic	V. papilionacea (2)	Introgressant (0)
Length/breadth ratio	.71 —1.00	.51 — .70
Length/length to lobe ratio	.65 — .80	.81 —1.00
Apical angle	66°— 85°	60°— 65°
Pubescence—upper lamina	0	1 — 3
Pubescence—lower lamina	0	1 — 3

Determining exactly what characteristics must be considered as typical of *V. papilionacea* was a difficult and often subjective task. Data were used from as many sources as possible. These included the original description of Pursh, modern manual descriptions, and, most important, measurements and observations made in the present population and herbarium studies. In working with the acaulescent blue violets, field work is absolutely essential, in the opinion of the authors, to a proper understanding of the nature of the different species. In the herbarium their morphological overlap often obscures their genetic relationships; in the field their ecological discreteness becomes apparent, as well as characteristics regarding general plant habit, flower color, and petal and leaf arrangement.

When plotted in bar diagrams (Figure 2) the distributions of hybrid index values for each population illustrate varying degrees of genetic disturbance. Five of the populations, 56-24, 56-31, 56-77, 56-17, and 56-22, have been apparently little disturbed by introgression from related species. The remaining four have been profoundly modified by introgression, probably principally (but not entirely) from *V. sororia*, the species most resembling the hypothetical "introgressant". It may even be debated whether or not a population such as 56-93 deserves to be called *V. papilionacea*.

Summary

A final table (Table 2) has been prepared to summarize the characteristics of *V. papilionacea*. It is based upon the population analysis discussed above and, in addition, measurements made of specimens from the University of Tennessee and the University of Minnesota. Among the more characteristic features of *V. papilionacea* are the following:

Pubescence—*V. papilionacea* is considered to be always completely glabrous. If pubescence occurs on the leaves, it is thought to be due to introgression from *V. sororia*. The majority of the stemless blue violets, both of woodlands and disturbed city habitats (in the midwest), are *V. sororia*, a species most easily distinguished by always being pubescent to some degree.

Lamina shape—By some authors *V. papilionacea* is said to have rather wide and blunt early leaves. This is exactly the opposite of the situation in the middlewest. As the length/breadth ratios in Table 2 indicate, the leaves are very nearly

as long as broad. In addition, the apices of mature leaves are somewhat attenuate and not at all blunt. In this respect they are similar to *V. missouriensis,* from which they differ in having the apices toothed with many small crenations.

Habitat—All the midwestern species of *Viola* are weeds occurring naturally only in disturbed habitats. *Viola papilionacea* is the weediest of all, being found exclusively in very sterile habitat conditions. In the midwest its favored habitat seems to be railroad roadbeds. Except where it is hybridizing with a woodland violet, it is found in the open. In towns and cities the commonest violet is *V. sororia,* but *V. papilionacea* occasionally grows beside sidewalks or roads.

Table 2

A Summary of the Characteristics of Specimens of *Viola Papilionacea* from the population samples and from herbarium material from Tennessee and Minnesota

Characteristic	Tennessee	Minnesota	Population Samples
Number of specimens	19	32	345
Lamina length		38.5 mm	52.4
Lamina 1/b ratio	0.96	0.95	0.88
Lamina 1/11 ratio	0.80	0.81	0.75
Apical angle	74.37°	70.91°	73.3°
Pubescence			
Above	0	0	0.40
Below	0	0	0.35
Margin	0	0	0.22
Petiole	0	0	0.17
Number of teeth	22.50	20.52	30.98
Petal pubescence[1]	0.05	1.00	—
Cleistogene position[2]	—	1.42	—

[1]glabrous—0, few hairs—1, very pubescent—2
[2]erect—0, ascending—1, prostrate—2

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Department of Biology
Grinnell College
Grinnell, Iowa