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A Hypothesis to Account for Unusual Leaf Variation in *Viola pedata* L.

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Abstract. Viola pedata L., the birdfoot violet, occasionally displays unusual variation in leaf shape in the southeastern United States. No satisfactory explanation for this has yet been provided. Analyses of variation in a colony with normal leaf shapes, one with the unusual leaf variants, and a neighboring population of *Viola primulifolia* L. subsp. *villosa* (Eaton) Russell leads to the hypothesis that the leaf variation is due to hybridization and subsequent introgression between *V. pedata* and *V. primulifolia* subsp. *villosa.*

The birdfoot violet (*Viola pedata* L.) is one of the most distinctive of North American species and is well known to eastern taxonomists. It is a "stemless blue" violet, the stem not extending above the surface of the ground. The corolla is usually some shade of blue. The leaves are nearly always deeply pedately cut into many linear segments. Perhaps its most notable variation is in the coloration of the corollas. These are either concolorous, all the petals being the same shade of blue (but this shade varying from plant to plant), or they are bicolorous, with the upper two petals much darker in tint than the lower three. The mechanism of inheritance of these color variations is very likely simple and of little evolutionary significance.

Variation in leaf shape and lobing is occasionally striking and may be of much greater evolutionary importance. The leaves of *V. pedata* vary in several ways. First, a single plant will usually exhibit marked leaf dimorphism. In early spring and late fall "juvenile" leaves (Figure 1*A*) will be produced; these have short, relatively wide, spatulate lobes. Throughout late spring and summer, longer, more deeply dissected leaves with linear lobes are produced (Figure 1*B*). A variety (*V. pedata* var. *lineariloba* DC.) has been based upon this summer leaf form. The difference in leaf shape seems, however, to be in large part a result of the photoperiod to which the plant is exposed and, hence, probably has no taxonomic validity (Russell, 1960).

From time to time colonies of *V. pedata* are found which exhibit a rather strange variety of leaf shapes (Figures 1*C* and 1*D*), to which a variety of names has been assigned. These colonies are not concentrated in any particular geographic area but occur rarely in

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the southeastern United States from Arkansas to Georgia and North Carolina.

In the spring of 1959 the authors became particularly interested in the cause of this odd leaf variation. This was principally due to a communication with Dr. Wilbur Duncan of the University of Georgia. We sought for plants with entire or slightly lobed leaves during a collecting trip in the southeast and examined a single aberrant colony, which was pointed out to us by Mr. Harry Ahles of the University of North Carolina. It was located seven miles east-northeast of Rockingham, North Carolina, beside U. S. Highway 1.

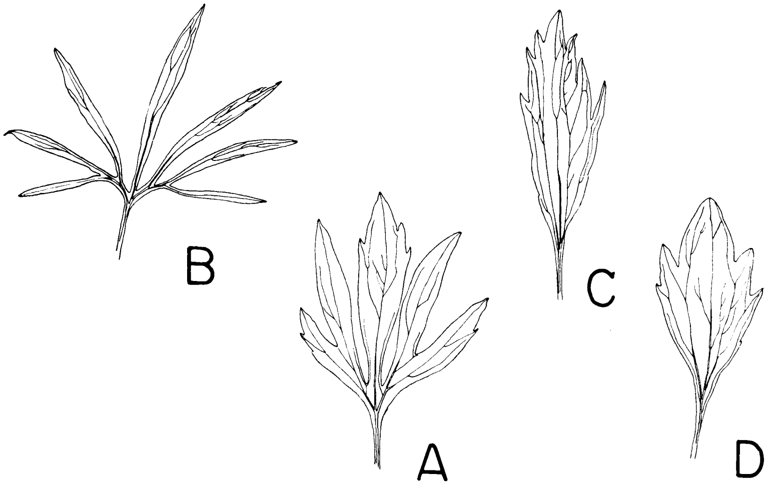

Figure 1. A—"juvenile" leaf of *V. pedata*. B—mature summer leaf of *V. pedata*. C and D—variant leaf shapes of *V. pedata* (from population WB-2).

Specimens from this colony and from other colonies of "normal" *V. pedata* were studied. We measured the leaves in our population samples and plotted the data on a pictorialized scatter diagram. Examining this diagram, we asked what species might have been responsible for the distribution of points, if hybridization and introgression had occurred. *Viola pedata* belongs to the subsection *Boreali-Americanae* of the section *Plagiostigma,* a group of violets noted for frequent introgression among the approximately 25 species.

No species of the *Boreali-Americanae* answered the description of our hypothetical introgressant. But a stemless white violet growing nearby seemed to fulfill the requirements of the missing parent very well. This was *V. primulifolia* L. subsp. *villosa* (Eaton) Russell (Figure 2). Initially, hybridization between these species seemed preposterous to us. *Viola pedata* has a chromosome number of n =

26, while *V. primulifolia* has n = 12. Although both belong to the section *Plagiostigma,* they are not, so far as is known, closely related. As the drawings (Figures 1 and 2) indicate, they are widely divergent in vegetative and floral morphology. On the other hand, close relatives of these two species have been known to hybridize successfully in nature. Brainerd (1909, 1924) reported natural hybridization between *V. brittoniana* Pollard and *V. lanceolata* L. in Massachusetts. The northern coastal plain form of *V. brittoniana* appears to be closely related to *V. pedata* (Russell, *ms.*), and *V. lanceolata* is the closest relative of *V. primulifolia* (Russell, 1955). Therefore it seemed worthwhile to test the hypothesis of introgression between these two species, to whatever extent our specimens and data would permit us.

Figure 2. *Viola primulifolia* subsp. *villosa.*

METHODS AND RESULTS

Analyses of three population samples are presented here: a collection of *V. pedata* exhibiting the normal vegetative morphology (WB-1), the unusual collection of *V. pedata* (WB-2), and the adjacent population of *V. primulifolia* subsp. villosa (NR 59-67). Specimens from each population were taken in the field, washed, pressed, dried, and later studied in the laboratory. Because neither flowers nor fruits were present on the specimens of *V. pedata,* only leaf characteristics were studied. These were:

lamina length
lamina breadth
lamina length/breadth ratio
actual surface area of the leaf ("real area")
area of the leaf surface plus the area of the inclosed sinuses ("outline area")
real area/outline area ratio (to indicate degree of leaf lobing)
pubescence of the upper and lower lamina surfaces, the lamina margin, and the petiole

Averages of several of the above measurements are presented for each of the three samples in Table 1. It is at once evident that the specimens from population WB-2 are intermediate. In addition, a hybrid index was prepared, using the following scale.

Table 1

Average Ratios and Measurements for the Three Populations

	WB-1 *V. pedata*	WB-2 *variant*	NR 59-67 *V. primulifolia*
Length/breadth ratio	0.79	1.81	1.96
Real area/outline area ratio	0.29	0.73	1.00
Total pubescence*	1.36	2.15	7.86
Pubescence upper lamina*	0.44	1.15	2.95

*Pubescence was scored on an arbitrary scale. For the entire leaf a value of 0 indicates glabrousness, of 8 very heavy pubescence. For the upper surface of the lamina 0 indicates glabrousness and 3 very heavy pubescence.

	V. pedata	*hybrid*	*V. primulifolia*
length/breadth ratio	0.25 – 1.50		1.50 – 4.00
real area/outline area ratio	0.10 – 0.40	0.41 – 0.75	0.76 – 1.00
upper leaf pubescence	0	1	2,3

Each plant was scored for each of the above three characteristics. A value of 0 was given for the extreme characteristic of *V. pedata,* a value of 6 for *V. primulifolia,* and a value of 3 for the hybrid. The distributions of hybrid index values for the three populations are plotted in Figure 3.

Conclusions

There is some rather convincing circumstantial evidence presented for the introgression of certain characteristics of *V. primulifolia* into *V. pedata*, as an explanation for the unusual leaf variation occasionally seen in populations of *V. pedata* in southeastern United States. This is summarized especially well in the last illustration (Figure 3). The distribution of hybrid indices for sample WB-2 may be especially revealing. It may be interpreted to indicate that, in this situation, the two modes of the indices represent modified genotypes of the two parent species which have drawn closer to each other by gradual, two-way introgression perhaps over a very long period. However, it must be emphasized that the present analysis deals only with a few selected leaf characters, and these may not be representative of the total genotype of each species.

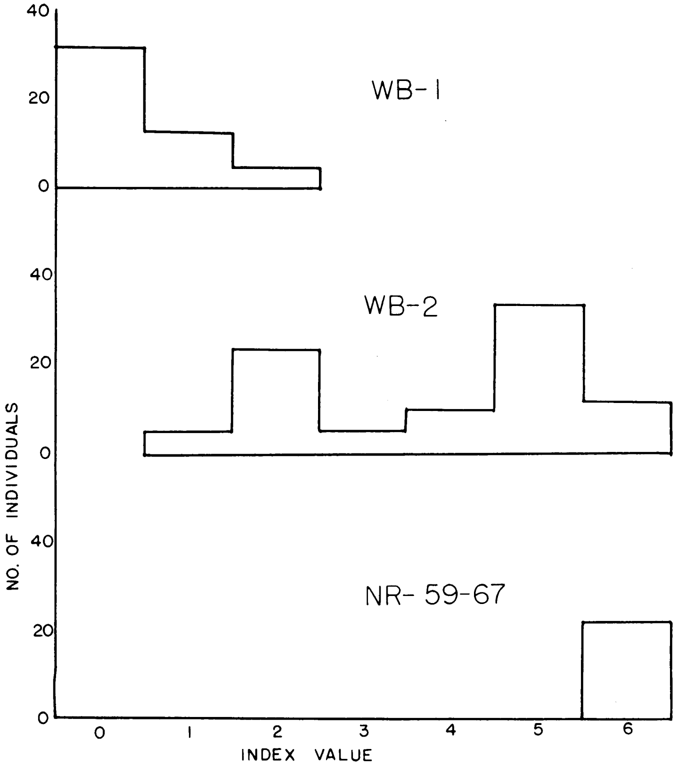

Figure 3. Bar graph summarizing distributions of hybrid indices in the three populations.

Efforts are being made by the authors to test this hypothesis further by the collection and examination of flowers and pollen and by transplantings. However, it may be some time before this can be completed, because of the difficulties in revisiting the localities and in growing *V. pedata* in the greenhouse.

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