HETEROPHYLLOUS LEAVES IN THE PALMATELY LOBED VIOLA EGGLESTONII BRAINERD

JESSE M. SHAVER

George Peabody College for Teachers

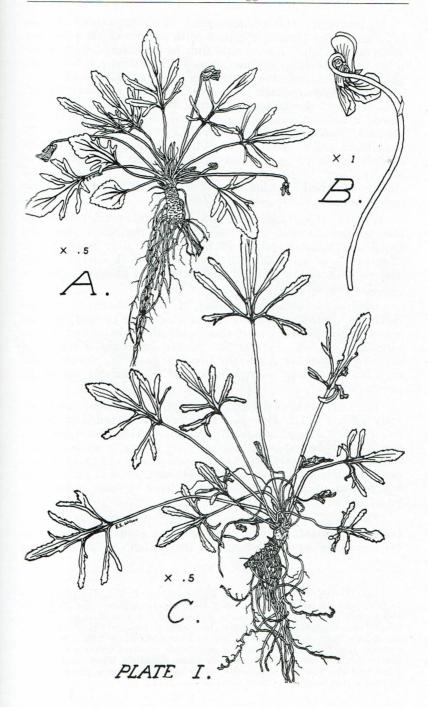
Nashville 5, Tennessee

Brainerd (1910b) points out clearly and skillfully the differences between heterophyllous and homophyllous and between pedately lobed and palmately lobed leaves. Heterophyllous violets have the earliest leaves of spring unlobed, later leaves lobed, and the leaves of late summer and autumn mostly unlobed. Homophyllous violets have leaves lobed and of essentially the same shape throughout the growing season.

The fundamental pattern of leaf lobing in the cut-leafed, stemless violets consists of three lobes: a single median segment and two lateral segments (one on each side). Each segment may be unlobed or dissected into additional lobes. When leaves have five or more lobes, they may be designated as either pedately lobed or as palmately lobed. Pedately lobed leaves have the median segment unlobed and each of the two lateral segments with two or more lobes. Palmately lobed leaves have the median segments with a lobe or lobes on each side and the lateral segments either lobed or unlobed.

Sometimes it is difficult to determine whether the lobing of a particular leaf is of the pedate or of the palmate type. Probably in all cases, the veining of the lobes would indicate their morphology. When the main vein of each lobe of each side of the median segment courses downward to join the main vein from each lateral segment to form a single vein that joins the midrib, the leaf is pedately lobed. These lobes are morphologically a part of the lateral segments even though they may appear to arise from the median lobe (Plate III, A). When the midvein of each lobe of the median segment joins the midrib separately from the main veins of the other lobes on that side, these lobes are morphologically a part of the median segment (Plate III, B). This leaf is therefore palmately lobed.

Plate I. (Opposite page.) Viola Egglestonii. A. Plant at spring flowering time, April 11, showing one unlobed leaf, many deeply dissected palmately lobed leaves, and some shallowly and pedately lobed leaves, no. 11092. B. Flower, no. 11091. C. Plant with all leaves deeply and palmately cut, no. 11219, May 17. Note, however, the second large leaf blade from the left with the veining of the left side indicating a pedately lobed leaf and the vining on the right side indicating a palmately lobed leaf.



In Brainerd's (1910a) description of V. Egglestonii, he has "... later ones [leaves] 3 parted with middle of all 3 primary segments 2-3 cleft." They would thus be palmately lobed. In another paper (1910b), Brainerd puts V. Egglestonii, V. Stoneana, and V. palmata together under the heading: "Leaves all palmately 5-11 lobed or parted, or rarely the first leaf of spring uncut." This separates them from the group having "earliest and latest leaves usually uncut, others pedately 3-7 lobed, -parted or divided," and comprising V. triloba, V. triloba var. dilatata, V. Lovelliana, and V. esculenta. Essentially the same characters were used by Brainerd in his treatments of these violet groups in Small's Flora of the southeastern states, 2nd ed., 1913, and slightly modified by Alexander in Small (1933), and in Brainerd's Violets of North America (1921).

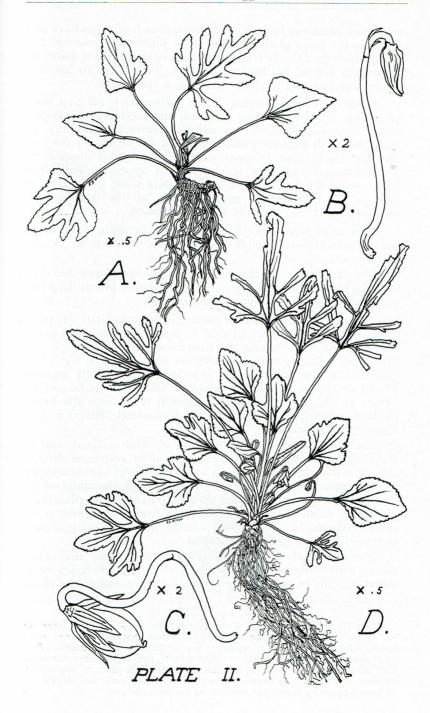
Fernald (1950) based his treatment of *Viola* mainly on Brainerd's studies but made little use of the leaf characters, palmately lobed and pedately lobed, in his key. He did, however, use "Leaves all or essentially all divided into 6-15 narrow lobes" (homophyllous) and "Leaves both lobed and unlobed" (heterophyllous) or similar phrases.

According to Brainerd (1910b), "It is noteworthy in our ten species of cut-leafed stemless violets, that those pedately cut are always heterophyllous, and those palmately cut always homophyllous" (p. 582). Farther on (p. 598) he modifies this statement by adding "or rarely the first leaf of spring uncut." This view has apparently been widely held by botanists up to the present time.

The fully developed spring plants of *V. Egglestonii* are palmately 5-lobed (Plate I, *C*) and have been so regarded by Brainerd (1910a) and other students of this species. Nevertheless, a careful examination of almost any early spring or autumn plant will disclose some pedately lobed leaves among the more numerous palmately lobed ones, and casual observation of early spring and of autumn plants showed the presence of some entirely unlobed leaves.

To check on this apparent seasonal appearance of unlobed leaves, I transplanted one plant into my garden, where it has been growing for four years, and three plants in a pan where

Plate 11. (Opposite page.) Viola Egglestonii. A. Late spring plant, June 16, with one old leaf palmately lobed, three leaves shallowly and irregularly lobed, and two most recent leaves unlobed, no. 11177. B. Cleistogamous flower, Oct. 1. C. An almost mature cleistogamous capsule, Oct. 1. (B and C are drawn from specimens preserved in formaldehyde solution.) D. A late autumn plant, Oct. 1. The five long and deeply dissected leaver are weather-beaten old hold-overs from spring; they are palmately lobed with the exception of no. 4 which is pedately lobed. The short leaves developed late and are either shallowly cut or unlobed, no. 11149.



they grew outdoors for one year. Numerous field trips have been made to the cedar glades (where these plants are common) near Smith Springs, Davidson County, and near Charlton Lane and Hurricane Creek, Rutherford County, Tennessee. In addition, I have available for study 50 herbarium specimens.

All of the plants growing in the garden have the first leaves of spring (1-5 in number) unlobed, the next leaves variously lobed (but mostly 5-lobed), and the leaves of mid-May and June mostly or entirely palmately lobed for nearly all the early unlobed leaves have by now yellowed, died, and disappeared. By mid-summer, the new leaves that are appearing have fewer lobes (some 5-lobed, some 4, some 3, and some 2-lobed) or no lobes at all. In favorable growing years, all the new leaves of late September and October may be unlobed.

Field trips indicated that the plants growing wild in the cedar glades showed similar types of leaves with similar seasonal appearances.

The leaf data on the 50 herbarium specimens has been brought together in Table 1 and representative plants have been sketched (Plates I-III) under my direction.

In general, the herbarium material indicates that: (1) plants at early flowering time (Table 1, April) have some unlobed leaves (Plate I, A) among the numerous lobed leaves; (2) mid-May plants usually bear lobed leaves only (Plate I, C); (3) by July and August, some of the new leaves are entirely unlobed; (4) all or almost all the new leaves of October may be unlobed (Plate II, D, and Plate III, C). Thus it seems that the heterophyllous condition is common on a seasonal basis for Viola Egglestonii Brainerd.

I believe that these leaves are normal and seasonal, and not the result of hybridization, because of their restricted distribution in cedar glades away from other species of stemless violets. Furthermore, the shape and cuneate base of the unlobed leaf does not suggest a particular hybrid parent. It is planned to grow some plants from seeds collected from cleistogamous capsules produced by plants known to be heterophyllous in order to settle the hybridization question.

It seems likely (based on casual observation) that plants during their first year from seed have most of their leaves unlobed. A study of such relations must be postponed to the future.

Plate III. (Opposite page.) Viola Egglestonii. A. A pedately lobed leaf, no. 11178. Veining from the upper lobes shows that they do not belong structurally to the median segment but to the lateral segments. B. A palmately lobed leaf, no. 11063. Veining from the upper lobes shows that they belong structurally to the median segment. C. A plant of late autumn, October 1, with all the deeply cut leaves dead and gone, no. 11050E. The 14 later appearing leaves are seen to be mostly unlobed.

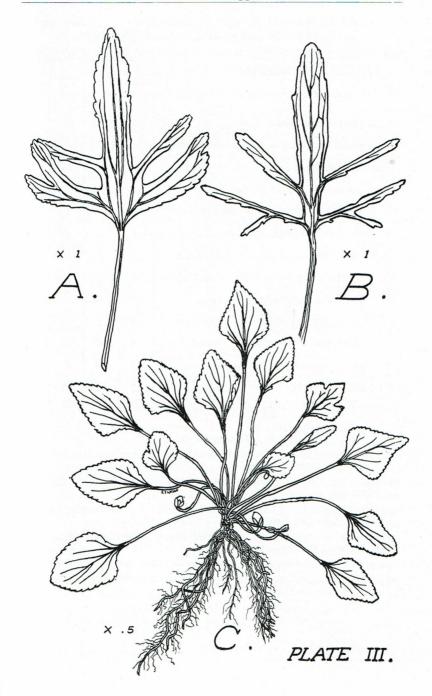


Table 1. Seasonal changes in abundance of certain leaf characters of Viola Egglestonii Brainerd

Leaf characters	Abundance changes			
	Apr.	May	July- Aug.	Oct
No. of plants having unlobed leaves	7	2	21	14
No. of plants having no unlobed leaves	2	1.	2	3
Total no. of unlobed leaves	20	4	37	78
No. of plants having 2: to 3-lobed leaves	1	0	7	11
No. of plants having no 2- to 3-lobed leaves	8	2	16	5
Total no. of 2- to 3-lobed leaves	1	0	10	28
No. of plants having pedately 5-lobed leaves	1	6	12	4
No. of plants having no pedately 5-lobed leaves	8	1	10	12
Total no. of pedately 5-lobed leaves	1	6	23	5
No. of plants having palmately 5-lobed leaves	4	2	4	5
No. of plants having no palmately 5-lobed leaves	4	0	19	11
Total no. of palmately 5-lobed leaves	19	10	11	14
Total no. of plants	9	2	23	16

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